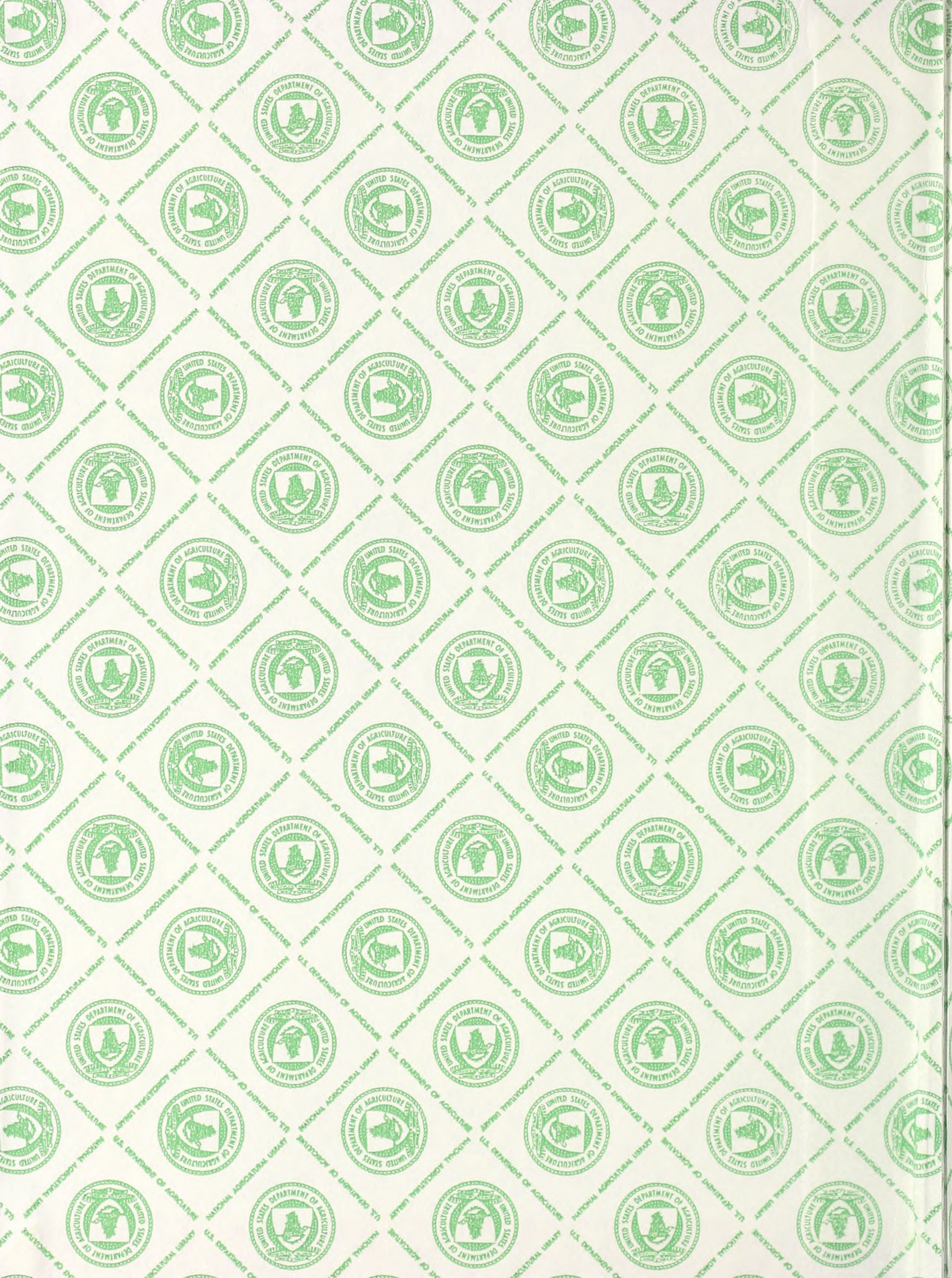


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Proceedings of The
**Symposium on Management of
Forest and Range Habitats
for Nongame Birds**

May 6-9, 1975
Tucson, Arizona



U.S. DEPT. OF AGRICULTURE
FOREST SERVICE
MAY 31 1975

Proceedings of The
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Issued July 1975



Dixie R. Smith
Technical Coordinator

Forest Service
U.S. Department of Agriculture
Washington, D.C.

Preface

Nongame birds are a neglected ecological and recreational resource. Managers have known that birds eat insects and seeds and that some people like to watch birds. But generally nongame birds have not been seriously considered in decisions on land management. Scientists, on the other hand, have long studied birds as an occupation or avocation, but they have seldom related their studies to land management activities. The recent increase in environmental awareness and dramatic changes in patterns of wildlife-related recreation are indicators that this Symposium was long overdue. Through it we have attempted to initiate a dialog between resource managers and avian ecologists.

The views expressed are those of the participants and not necessarily those of the U.S. Department of Agriculture. Neither does the use of commercial names constitute an endorsement by the U.S. Department of Agriculture.

The following organizations joined the Forest Service in sponsoring the Symposium: Arizona Game and Fish Department; Fish and Wildlife Service; International Association of Game, Fish, and Conservation Commissioners; National Audubon Society; Wildlife Management Institute; University of Arizona; and the Wildlife Society.

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Tuesday Morning, May 6

General Session

*Presiding: T. C. Nelson
Forest Service, USDA*



Keynote Address:

The Challenge of Practical Ecology¹

John S. Gottschalk ^{2/}

The subject of this symposium, "Management...for Nongame Birds," seems to signal a new emphasis, or direction if you will, in wildlife management thinking. New directions, which tend to suggest the possibility of exploration into unknown areas of human activity, are always exciting for both participants and onlookers; so I was stimulated and enthused by the thought that someone was concerned about the broad aspects of the management of nongame wildlife on forest and range lands. The idea, and a discussion of it, is particularly intriguing in view of the fact that many of us in the wildlife conservation profession have thought for several years that our programs have been too game oriented for too long.

It is easy to understand and explain our traditional preoccupation with harvestable wildlife. It is rapidly becoming more difficult to justify the tradition. Historically the hunter and the fisherman have paid the bulk of the bill for our wildlife conservation efforts. It is noteworthy but of little practical consequence that many of those who are not "harvesters" of wildlife and thus its financial supporters would like to help pay the bill. The fact is that our national sensitivity to the wild biota which surrounds us is basically attuned to those life forms which have some immediate significance to man's more material, if not his pecuniary interests. That is to say, if a particular species can be exploited we find ourselves studying it and attempting to manage it in order to expand its contributions to man's welfare. The

reciprocal of course is also true: if an animal poses a threat to man's interests, his health, his safety, or to his pocketbook, again the species commands attention and programs are built to control it.

Thus, in a sense, one could characterize wildlife-management policies over much of the world, as a matter of fact, as being superficial. They deal largely with end products, and ignore the vast and complex matrix of plant and animal life which in the long run supports not only fish and wildlife but man himself. It seems then that the significance of this symposium may dwell in what it may do first to emphasize the need for a broad concern for all kinds of things that live in forests and on range lands; and secondly, what we can do, given the kind of a place the world is today, to cause this concern to be directed into management programs.

There is an exception to every rule. In this case it is the phenomenon of the growth of the popular and sentimental concern for the protection and preservation of endangered species. This phenomenon runs counter to the premise that we have worked almost exclusively on game or useable wildlife, but reinforces my hypothesis that we are overlooking many of the most important elements in the natural systems which support living things generally. In other words, the concerns about endangered species are as narrowly focused as those supporting game-wildlife programs. For years the Fish and Wildlife Service and the bird conservation groups have capitalized on the whooping crane as a propaganda tool to build a public awareness of the need for wildlife conservation. The result is that the whooping crane has become a veritable symbol of our efforts at environmental and conservation redemption. Similar public attention is now being cultivated on behalf of the cetaceans.

^{1/}Keynote address at The Symposium on Management of Forest and Range Habitats for Nongame Birds, Tucson, Arizona, May 6-9, 1975.

^{2/}Executive Vice President, International Association of Game, Fish and Conservation Commissioners, 1412 16th St., N.W., Washington, D.C. 20036.

Earlier I commented that we were excited by the subject for this symposium in the sense that it suggested we might be headed in a new direction. In the course of preparing these remarks I leafed through a copy of the "Wild Life Handbook" of the Forest Service's North Central Region Nine, with headquarters in Milwaukee, published in 1936. This handbook was given to me as a young biologist for the practical guidance it contained. Listen to this from the foreword by Regional Forester Tinker:

"In the management of National Forest lands, the production of Wild Life will be correlated with the production of other resources and its importance will be recognized regardless of whether or not there is a direct monetary return to the Federal Government."

And from Objective and Policy, III:

"The great economic and social values of wildlife in the National Forests demand that attention be given this resource in proportion to its desirability and need.

"The degree of desirability and importance will be shown by the public demand, as indicated by the use of wildlife resources. Animal resources in inaccessible areas or far from centers of population are used but slightly by the public and will need little or no attention in comparison with forest areas near centers of population where demands for animal products are intense. In the latter locations the priority of wildlife activities will be high."

And finally, under Objective IV:

"Priority in the Management of Species.

A. Animals that are in danger of extinction will have priority on restricted ranges over all other wildlife resources.

B. Where two species of animals of equal importance are competing for the same range, the one having the most exacting life requirements will have preference over one with greater tolerance as to life conditions.

C. Management procedures for species other than included under A and B will be on the basis of the demand as indicated by the greatest good to the greatest numbers."

This material demonstrates first that the Forest Service was concerned about endangered species forty years ago. It had translated that concern into official policy and a management handbook, hopefully used by foresters throughout the Middle West. But secondly it reinforces the first of my basic premises, that the use of wildlife resources is the measure of their value. Again, it is this philosophy which has dominated public and political wildlife resources policy over the years. The "use syndrome" in its most material sense has become the cornerstone of our wildlife programs. Given the great increase in human populations, and the consequent intensification of use of our wild and cultivated lands, that cornerstone may be on a shaky foundation.

If the concept of direct and material utility as the basis for wildlife management is inadequate, it is axiomatic that we must substitute some other rationale. Given the nature of our society and its systems for ordering priorities, at some point we will be called upon to justify a philosophy that attempts to give significance to species of wildlife which have no apparent utility. Thus while the question, "Why manage for nongame wildlife?" may appear to be academic it is nevertheless a highly necessary one. In the absence of visible utility, what alternative exists? It would seem that this question cannot be approached save in the broad framework of ecology.

We all remember Barry Commoner's Four Laws of Ecology:

1. Everything is connected to everything else.
2. Everything must go somewhere.
3. Nature knows best.
4. There is no free lunch."

Translated into other terms, these truisms promise that we will pay heavily and perhaps in ways we cannot imagine if we fail to maintain the basic genetic diversity which characterizes our wild living resources; that the animal-plant community relationships, in other words, the biotic basis of our wild resources must be sustained. The reciprocal implies a reward: that husbandry of our wild heritage will produce both tangible and intangible benefits, partly in the immediate or potential production of substance or activity of economic significance to man.

Writing in the March 1975 bulletin of the IUCN, Robert Allen comments:

"If we are not to greatly restrict our capacity for developing new products, we need to retain large areas of undisturbed habitat, particularly of tropical forest. Tropical forests are rich stores of diversity, containing potential foods, drinks, drugs, medicines, gums, resins, specific pesticides and other chemical compounds. Discovering and developing them is an enormous task--inventing them would be impossible. We should not forget that the chemical clues leading to the development of a great many synthetics--from aspirin to the oral contraceptive--were discovered from plants. Tropical trees, thanks to their constant battle with herbivores, are source-books of chemical invention, of which man has scarcely turned the pages."

If we can accept the premise that management of our forest and range lands for nongame wildlife as well as game and endangered species, that is on an ecological basis can be "sold," we come to an almost overwhelming problem: how to go about it? The fact is, of course, that very little ecological management has taken place. The record shows that most such management is essentially single-purpose.

The primary dilemma of the wildlife manager who concerns himself with non-

game wildlife is simply the lack of knowledge essential to construct accurate and adequate biotic models. Nor have we developed the ecologically sophisticated managers essential to respond to the challenge of ecosystem management.

Before we can come to any reasonable state of competency in the decision making levels of the responsible organizations many fundamental changes will have to be made. These range from shifts in policy concepts that must be accepted by the public and structured into our basic land- and water-use programs, all the way to the mandating of an educational policy that emphasizes ecological concepts in our basic educational system. Several specific changes are needed.

The country needs to develop and espouse a broad policy which will make possible the management of our land so that its basic contributions to the environment will not be jeopardized. Maintenance of a productive earth is just as fundamental for people, endangered species, game wildlife, and fish, as it is nongame wildlife.

Our basic national policy must, within the broad guidelines above, provide means to protect and retain smaller areas needed by individual species and their associated biota.

We must recognize that our knowledge of the enormously complicated "web-of-life" is far too limited to support an ecological approach, and that a material expansion of research into the broad area of ecological relationships is essential.

We must revamp our basic educational programs and especially our wildlife manager training programs to produce professionals who have an ecological awareness. We are still producing far too many graduates who are primarily fish and game management technicians whose jobs are to make more deer or turkeys, or whatever is listed in the legal bag, available to the license buying sportsmen.

With all of these broad problems that must be faced on a philosophical or policy basis, the challenge to the field manager--the practical ecologist--seems almost monumental. He faces

situations in which there are severe policy discrepancies, fragmented programs, inadequate knowledge, and poorly trained personnel. Obviously, most of these problems must be attacked by the policy maker rather than the land or wildlife manager himself.

The manager, faced with the responsibility for managing nongame wildlife, could well begin by remembering what Aldo Leopold said, "The first rule of intelligent tinkering is to save all of the pieces." But all the maxims in the world will not be of much assistance to the practical manager challenged with the need to employ an ecological approach. He takes a look at his forest, his "range," or his marsh and says to himself, "I must find a way to run this place ecologically! That means I must analyze the effect of whatever I choose to do on all the life forms present here." Obviously, he must immediately start the complicated process of choosing from a series of alternative actions, by far the largest part of which are based on assumptions. He soon realizes that at some level, probably not too far down in the biotic pyramid, he will conclude that he must stop the process or become mired in overwhelming detail. The challenge is in devising a means of deciding where to draw a reasonable line between the possible and the desirable. The manager who concerns himself with an ecological approach will find himself impaled on the horns of this dilemma with monotonous regularity; but realistically, it is the lot of all managers to make and live with these difficult choices.

The foregoing thoughts have been put into much more sophisticated language as a result of a recent series of conferences on the theory of "Maximum Sustained Yield" sponsored by the World Wildlife Fund, the Council on Environmental Quality, the Smithsonian Institution, and the Ecological Society of America. The conferences produced a paper outlining four general principles which resource managers are urged to adopt. As general principles they cover the management of resources wherever they may be found. The principles are:

"1. The ecosystem should be maintained in a desirable state such that

(a) consumptive and non-consumptive values can be maximized on a continuing basis

(b) present and future options are ensured

(c) risk of irreversible change or long-term adverse effects as a result of use is minimized.

2. Management decisions should include a safety factor to allow for the facts that knowledge is limited and institutions are imperfect.

3. Measures to conserve a wild living resource should be formulated and applied so as to avoid wasteful use of other resources.

4. Survey or monitoring, analysis, and assessment should precede planned use and accompany actual use of wild living resources. The results should be made available promptly for critical public review."

To sum up, I fear that we have not yet reached the point in our public attitudes toward wildlife, where we can assume support for fish and wildlife resources that have no obvious utility. Therefore the best approach will be to attempt to tie programs for nongame species into an overall ecological orientation. To do so will require changes in public policy dealing with our renewable wildlife resources, and in the system of training land and wildlife managers. Meanwhile such managers must do their best to become practical ecologists.

Doubtless we shall hear more about these things in the next few days as the various speakers at this symposium speak both generally and specifically on their assigned topics. None of us expects that this symposium in itself will ultimately be called a revolution in living resource management thought, but one may hope that it will one day be recognized as having been a part of the opening skirmish in such a revolution.

Economic Values and Recreational Trends Associated With Human Enjoyment of Nongame Birds¹

Brian R. Payne^{2/} and Richard M. DeGraaf^{3/}

Abstract.—Total direct expenditures for the enjoyment of non-game birds in 1974 were estimated to be \$500 million. Expenditures for birdseed, binoculars, and camera equipment constituted 95 percent of the total. Continued moderate growth is predicted.

INTRODUCTION

One measure of the importance of any resource is its economic value; another is the number of people who use that resource. The enjoyment of non-game birds is generally agreed to be an increasingly important recreational activity, perhaps rivaling hunting or fishing in economic importance or numbers of participants. But estimates of economic values and numbers of participants are difficult to make and are scarce. Forest, range, and other land managers need better estimates of these values to help them decide how much effort to devote to management of non-game birds.

Perhaps we should first answer the question, "Why measure the economic values of non-game birds?" After all, the benefits from enjoying non-game birds are intangible, and it may seem a shame, if not impossible, to express these benefits in monetary units. But in our society, dollars talk! Even though we recognize that

the value of a resource, product, or service arises from its use or from its exchange for other goods or services, we usually express this value in terms of dollars and cents. Economic value may be a crude and imperfect measure of worth, but it is a useful means for comparing different kinds of goods and services, even if some of them are intangible.

We have attempted to measure economic values associated with non-game birds in order to demonstrate the importance of a resource whose existence has only recently been admitted by many forest, range, and wildlife managers. So pay attention; birds may be worth more than you think to the American public.

Because the benefits of bird watching are intangible, their dollar value must be estimated by one or more indirect methods, all of which have disadvantages relative to market pricing. (See Ashton et al. 1974, Halvorsen et al. 1972, and Horvath 1974, for some examples of valuation methods applied to wildlife.)

We estimated direct expenditures associated with the enjoyment of non-game birds as the most conservative measure of their importance. Included in our estimate were total retail sales of birdseed, birdhouses and feeders, field guides, gift books, a portion of total retail sales of binoculars and cameras, and dues paid to bird conservation societies.

^{1/} Paper presented at The Symposium on Management of Forest and Range Habitats for Non-game Birds, Tucson, Arizona, May 6-9, 1975.

^{2/} Principal Forest Economist, USDA Forest Service, Northeastern Forest Experiment Station, Amherst, Massachusetts.

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A common shortcoming of an expenditures approach to measuring the value of an activity is the tendency to overestimate value by including indirect expenditures. We did not include expenditures for transportation, lodging, food, alcoholic beverages, or clothing used during bird watching expeditions. Although often associated with bird watching, these expenditures are made primarily for their own sake and are not required for enjoyment of wildlife. Thus, our estimate probably represents a minimum value for expenditures related to bird watching.

CATEGORIES OF EXPENDITURES

Expenditures for wild birdseed are directly attributable to enjoyment of non-game birds. Virtually no uses exist for birdseed apart from feeding birds. Birdseed is purchased and consumed annually; dollar sales thus represent a measure of current interest in non-game birds. Our estimates ignore expenditures for wildlife foods other than birdseed, such as breadcrumbs, table scraps, suet, and grains purchased from feed stores, but not identified as birdseed. In dollar terms, this omission is of minor importance.

Birdhouses and feeders are a second category of expenditure related directly to the enjoyment of birds. Often a nest box or feeder will be the first purchase by a new bird watcher. Because these items last for many years, current purchases may underestimate the interest in bird watching. Also, many houses and feeders are homemade, and we did not estimate the cost of materials used to make them.

Expenditures for guides to the field identification of birds are also directly attributable to non-game bird enjoyment. A few titles account for the great majority of sales. Because each book lasts for years, annual sales are attributable primarily to recruitment of new bird watchers. However, most serious bird watchers own at least two different guides.

Gift book purchases are attributable primarily to wildlife appreciation, although some people may buy books as status symbols, or they may give them as gifts whether or not the recipient has any interest in birds. Although each book has an indefinite life span, many people collect the new titles available each year. In this sense, gift books are consumed annually, and the sales of the new books each year are a good measure of current interest in wildlife.

Membership dues paid to organizations such as the National Audubon Society are easily estimated. They show a continuous record in the numbers of people interested in birds and other non-game wildlife.

A portion of the annual retail sales of binoculars is directly related to wildlife appreciation. No serious bird watcher is without at least one pair of fairly expensive binoculars that he uses almost exclusively for identifying and observing birds. Because a good pair of binoculars lasts for decades, sales are attributable primarily to recruitment of new bird watchers.

A portion of the market for photographic equipment is directly attributable to appreciative uses of wildlife. As with binoculars, the trick is to estimate what portion. Most serious bird watchers own one or more cameras; however, these probably are not used exclusively for taking pictures of wildlife. Because the market for camera equipment is huge, even a small percentage attributable to wildlife appreciation represents a large annual expenditure.

We did not attempt to estimate expenditures for several other items that might reasonably have been included. Not included were memberships in countless state and local birding organizations, sales of records and tapes of bird calls, expenditures for courses on bird identification, sales of art work related to birds, or entrance fees to bird and wildlife sanctuaries.

EXPENDITURES IN 1974

Several studies have contributed to our knowledge of the annual expenditures for birdseed. Forty-three percent of households surveyed in Amherst, Massachusetts fed birds in 1972 (DeGraaf and Thomas 1974). A survey of Massachusetts residents (Massachusetts Audubon Society 1974) found that one-third of all households bought an average of 60 pounds of birdseed per year. A survey in Maine that was admittedly biased in favor of persons interested in birds found that one-third of all households fed nearly 125 pounds of birdseed per year (Cross 1973).

Birdseed purchased by percent of households in five major cities in 1972 is shown in the following tabulation (Bruce Dunning, AGWAY, Inc., personal communication, March 1974):

<u>City</u>	<u>Percent of households that fed birds</u>	<u>Pounds of seed purchased per household</u>
Boston	23.8	69.6
Cleveland	24.7	57.6
Milwaukee	19.4	64.5
New York	15.1	49.2
St. Louis	19.8	64.5

Based on these studies and on communication with birdseed suppliers, we concluded with considerable confidence that approximately 20 percent of U.S. households purchase an average of 60 pounds of birdseed per year; furthermore, these figures have remained constant for several years. Based on an average retail price of \$18 per hundred-weight in 1974 and approximately 15 million households feeding birds, we calculated that total annual retail sales in 1974 were \$170 million.

Sales of birdhouses and feeders are more difficult to estimate accurately than sales of birdseed. Annual sales are much lower, and dozens of small companies make birdhouses and feeders. Based on annual sales and estimated market percentage of one large supplier, we estimated expenditures of \$15 million for birdhouses and feeders in 1974.

Sales of field guides are dominated by two publishers. Based on communication with these publishers, we estimated total sales of five titles at \$3 million in 1974.

Sales of gift books about birds were slightly over 4 million dollars in 1974, according to figures that we obtained from a private market research firm (Jerome P. Harkins, personal communication, January 1975).

Based on membership records, we calculated dues paid to the National and the Massachusetts Audubon Societies totaling \$3.1 million in 1974. This amount under-represents total dues paid to organizations primarily concerned with non-game birds, but by an unknown amount.

Bird watching accounts for between one-half and two-thirds of total dollar sales of binoculars. Birders buy very few binoculars in low price ranges, but may buy as much as three-quarters of the binoculars that cost more than \$250. (These figures are based on warranty return cards and were adjusted for non-response

in lower price ranges.) In 1974, approximately \$115 million were spent by bird watchers for the purchase of binoculars.

Data on camera sales attributable to non-game bird photography are extremely difficult to obtain, partly due to the large number of foreign and domestic camera makers and to the wide range of subjects photographed. The latest figures available showed total sales of cameras, lenses, film, and photo processing to be about \$3.7 billion in 1972. We attributed four percent of this total to photography of birds, and we estimated an expenditure of \$190 million in 1974.

Thus, the total direct expenditures attributable to the enjoyment of non-game birds in 1974 appeared to be about \$500 million. Photographic equipment and services, birdseed, and binoculars account for 95 percent of this total. An additional three percent is contributed by birdhouses and feeders, with minor contributions from membership dues, gift books, and field guides.

Our estimate of \$500 million per year is both a conservative and an impressive indication of the economic importance of non-game birds. To help put this figure in perspective, compare it with the total expenditures of hunters exclusive of transportation, lodging, food, and alcoholic beverages. According to the 1970 National Survey of Fishing and Hunting (USDI 1972), this total was \$1.7 billion.

Or, compare birding expenditures to expenditures of waterfowl hunters, since their target is also birds. In 1970, waterfowl hunters spent \$180 million, excluding transportation, lodging, food, and alcoholic beverages (USDI 1972). If we allow for inflation and some increase in hunting by 1974, waterfowl hunting expenditures were probably about \$300 million, or 60 percent of birding expenditures for the same year.

We do not mean to suggest that birding and hunting are antagonistic forms of recreation, or that they are substitutes for one another. Our point is merely that by the criterion of total expenditures, birding was more highly valued than waterfowl hunting in 1970. This fact may surprise some wildlife managers.

TRENDS IN EXPENDITURES

Not only are expenditures for non-game bird enjoyment impressively high, but they have been increasing rapidly in the past several years. For example, gift bird-book sales were

only \$1.5 million in 1970 but \$4 million in 1974. Dues paid to the National and Massachusetts Audubon Societies doubled in five years, increasing from \$1.6 million in 1970 to \$3.1 million in 1974. Field guides have shown a steady, although not a dramatic growth in sales.

Sales of birdseed have risen from \$50 million in 1969, to \$80 million in 1972 to \$170 million in 1974. The latter increase is attributable almost entirely to a doubling of the price of birdseed from 1972 to 1974. The failure of consumption to drop in response to this price increase is surprising. Apparently the demand for birdseed is inelastic at current price levels. This suggests (1) that consumers consider bird feeding to be very important, (2) that birdseed is underpriced in relation to the value received from feeding birds, or (3) that people who feed birds are wealthy enough that they did not mind spending an average of \$10.80 in 1974 for birdseed that cost them only \$5.40 in 1972. In any case, expenditures for birdseed seem likely to continue to rise, even if the quantity sold remains constant.

BIRD WATCHING AS RECREATION

The popular image of bird watching is at striking variance with reality. Often viewed as the province of timid, frail old ladies, bird watching can be a hardy and rugged activity. Serious bird watchers may equal hunters in stamina, and they may exceed them in knowledge of the out-of-doors.

The typical bird watcher is male, white, married, above average in education and income, and is either retired or a young professional (Horvath 1974).

However, bird watchers vary in skill and intensity of interest from casual amateurs to dedicated professionals. Many people are content simply to learn the birds that use their window feeders. Others own field guides and binoculars, take birding walks, and maintain a list of birds identified. Still others own expensive photographic equipment, travel for the express purpose of sighting new or rare species, and are experts on bird ecology and biology.

The recent sighting of a Ross's gull near Boston illustrates the extreme dedication of many bird watchers and the degree to which they will spend time and money to pursue their hobby (Boston Globe, March 9, 1975, p. 1). Up to 1,000 bird watchers per day flocked to Newburyport, Massachusetts to see this extremely

rare bird. They drove from Bangor, Buffalo, Baltimore, Kentucky, and Tennessee. Others flew in from Florida and California. Secretary of Defense James Schlesinger, an avid bird watcher, arrived from Washington, and a business executive returned immediately from South Africa to see the only North American bird that he had not previously seen.

TRENDS IN RECREATION

It is difficult to measure the trends in recreation associated with non-game birds. No license is required for bird watching, it can be enjoyed anywhere, and it can be carried on simultaneously with activities such as hiking, camping, or auto travel.

The 1970 National Survey of Fishing and Hunting (USDI 1972) states that the number of bird watchers declined from 10 million in 1965 to 7 million in 1970, while the number of bird and wildlife photographers increased from 3 million to 5 million. We suspect that the trends revealed in these figures are the result of changes in definitions or sampling techniques rather than real changes in the population. For example, only 8 million bird watchers were reported in 1965 (Davey 1967), based on the same survey that led to the 10 million estimate for the same year. And remember that 12 million households bought birdseed in 1969, 14 million in 1972. Since there is likely to be at least one bird watcher in each of these households, we believe that most previous estimates of numbers of bird watchers are too low.

Rapidly growing interest in non-game birds is suggested by membership in the National Audubon Society, 41,000 in 1963, 142,000 in 1970, and 321,000 in 1975. This was an eight-fold increase in 12 years.

Growth in subscriptions to National Wildlife magazine was cited in 1967 (Davey) as an indication of changing public attitude toward wildlife, from consumptive to non-consumptive use. In 1967, subscriptions had grown to 250,000, from 60,000 in 1963; there were 350,000 subscribers in January 1975 (National Wildlife Federation, personal communication, March 1975). Ranger Rick now goes to 500,000 children; its second issue, in January 1975, went to 35,000 (Davey 1967). We think that many of these children will grow up with a greater appreciation than their parents had for birds and other non-game wildlife.

RECREATION IN THE FUTURE

Our crystal ball tells us to expect an increase in recreation associated with enjoyment of non-game birds, both in absolute amount and relative to consumptive wildlife activities. But it also warns us not to expect unlimited recreation growth.

As our population becomes more urban, better educated, and enjoys higher real income, it will look more to non-game wildlife and less to hunting for recreation (Hendee 1965; Hendee and Potter 1971). More non-game wildlife recreation means more bird watching, particularly by urban residents. Wildland managers should expect an increasing percentage of recreational visitors to be bird watchers, even if total use does not increase. Urban land managers should prepare for a relatively greater increase in bird watchers, and they should alter their management practices wherever possible to improve habitats for non-game birds (Thomas and Dixon 1973).

Although an increase in bird watching and other non-game wildlife recreation seems certain to occur in relative terms, we are unwilling to predict substantial and continuing growth in absolute numbers of bird watchers or visitor days of recreation.

Population growth is slowing, the energy crisis will continue to restrict travel, and world economic conditions imply a sharp change in our expectations of a continually rising standard of living. These factors will combine to depress growth in outdoor recreation activities requiring travel. And the question has been asked whether we are headed toward a society of leisure or a future characterized by a scarcity of leisure time (Zuzanek 1974). Zuzanek suggests that industrial societies may have reached an equilibrium point, beyond which further substitution of leisure for income will not occur. He further suggests that "Maintenance-nurturance activities such as sleep, hygiene, child care, and household obligations" compete with leisure activities (including recreation) for the use of non-working time (Zuzanek 1974:293).

CONCLUSION

Thus, we predict moderate increases in the economic importance and the recreational activity associated with non-game birds. A substantial portion of these increases will occur at the expense of other recreation activities, including hunting. Non-game bird enjoyment is already an important activity, but expenditures for management of birds and their habitat are very small relative to expenditures for game

management. We suggest that additional funding, perhaps from new sources, is needed to support greater management of and research on non-game birds.

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Direct Interactions Between Humans and Birds¹

Fred G. Evenden^{2/}

Abstract.---Presents an overview of relationships between humans and birds in early history and modern times. These relationships are discussed in terms of pleasure, profit and pain to humans and concludes on human actions detrimental to birds.

INTRODUCTION

The assignment of this extremely broad topic leaves me wide open as to the ground to be covered. I first considered a highly scientific presentation based upon the premises that everything on earth is connected to everything else, and that for every action, sooner or later there must be a reaction. Thus, if insectivorous bird populations are removed from an area, undoubtedly there will be an insect outbreak, or if an area of woody vegetation is converted to grassland, the faunistic composition of that area will be changed significantly, and so on. However, the many highly technical presentations ahead of you this week on such subjects as behavior, migration and energy flow, helped me decide to take a different tack.

A broad scan of the diverse range of interacting and somewhat philosophical relationships between man and birds seems appropriate. This review will treat all birds generically, whether they be game or nongame forms. The criteria for classification of birds, and for their very existence, are essentially biological. I am sure you will see this borne out in almost all of the habitat management papers this week. The artificial classification of game or nongame birds is, after all, subject to the long-term whims, mores, and actions of civilized and uncivilized

man.

It is hoped this broad-brush approach will serve to give forest and range land managers at least a brief insight to the diverse ways in which birds have stimulated both actions and reactions within man. These may help managers to better relate to people whom they serve in carrying out their responsibilities in nongame bird management.

BIRDS AND EARLY HISTORY OF MAN

Historically, there were both practical and impractical relations between man and birds. Early man undoubtedly relied on wild birds as a major source of meat. For thousands of years, birds were mysterious, subjects of awe, and of worship. They earned a place in biblical history in Genesis and many other books of the Bible, and it was reportedly a dove that brought a twig back to Noah after the mighty flood. Early cultures passed along to us many references to birds through their statuary, ceramic and painting arts. In more modern times, musical compositions have included birds in "Bye Bye Blackbird," "La Gollondrino" (The Swallow), "Yellow Bird" and the "Turkey Trot." Birds are featured in the works of many of the world's outstanding poets: "To a Waterfowl" by William Cullen Bryant, "Ode to a Nightingale" by John Keats, "The Raven" by Edgar Allen Poe, "Hark! Hark! the Lark" by William Shakespeare and "To a Skylark" by Percy B. Shelly.

As languages have developed, birds have acquired their fair share of identity within at least our own English language. Among these aveomorphic (and you will not find that in the dictionary!) interpretations of man are 'early bird,' 'birdbrain,' 'jailbird,' 'chicken,' 'vul-

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ture,' 'hawk,' and 'dove.' Golfers have their happiness expressed in 'birdie's' and 'eagle's.' Each of you may think of other birdy applications such as 'dead as a dodo,' 'birds of a feather,' 'its for the birds,' and 'a bird in the hand.'

It would be a shame to close this historical scan without pointing out that a nongame bird, the bald eagle, won out in Congress by one vote over a game bird, the wild turkey, as this nation's symbol.

And speaking of symbols, perhaps our most pressing environmental management problem can be blamed on another nongame bird, the white stork, bearer of newborn humans!

BIRDS AND MODERN MAN

As one considers relationships of birds and man today and in "recent" yesterdays, these relationships seem to fall rather conveniently into three P's--Pleasure, Profit and Pain, with losses or damaging or harmful actions wrapped into "pain." It must be pointed out that these artificially separated categories are quite often interwoven into inseparability.

Pleasure

Birds certainly fulfill the synonyms of "pleasure" for humans. They bring happiness, delight and enjoyment. They have been given recognition over the centuries in the previously-mentioned audible, legible and visual arts created by man.

Sight and Sound.--However, birds themselves are highly audible and visual arts of God. My wife and I, after living more than a decade with beautiful cardinals and blue jays year round in our yard, wonder just how less pleasurable some future homestead of ours may be without them. Most humans fortunate as we to have a wonderful collection of songsters around them must agree they are enjoyable. Some of us believe the beautiful summer-night-long song of the mockingbird or yellow-breasted chat far outweighs the negative aspects of whatever sleep-disturbance factors may be involved. Those less fortunate who must find their garden habitats in public parks or woods often have related their visits to me in terms of prominent memories about the birds or other animals they saw there. The parks themselves had faded away. Birds are not only colorful and tuneful, but just plain interesting to most people. Who cannot take notice of the calling geese as they pass overhead in migrating

vees? Further, when friends or strangers learned of my own interest in birds, they usually started a discussion about a bird experience or question they had. I believe we wildlife managers have missed all-too-many opportunities to utilize these natural human interests in birds to inform our fellowman about the purposes of and needs for management of natural resources. Much of the blame for the public anti-hunting attitude today can be placed on this failure. These same humans, perhaps looking to that someday when they might experience the sights and sounds of certain birds, join strongly these days in support of preserving threatened and endangered species of wildlife.

Captives.--Humans achieve vicarious pleasure from birds held captive. These may be cage birds in the home such as macaws, parrots, parakeets, mynahs, canaries and other finches. They may be so held for their beauty, voice or actions. Others enjoy watching birds in public and private zoos and aviaries.

Recreation.--In addition to such on-the-spot pleasures derived from birds, there are other, more energetic ways in which birds are related to man's recreational pursuits. Sport hunting for birds has been an established custom for centuries. Through falconry, birds replace arms as a means of taking.

The much more recent hobby of birdwatching has stimulated new millions of humans to move beyond their domiciles, even to the farthest corners of the earth, to locate, observe and record with binoculars, cameras and notebook the species found there. Many of these pleasurable activities have produced scientific data, as well as pleasure for other than the traveler through the printed page and recording media.

Birdwatching is a healthful hobby that has developed demand for skills not previously well-recognized in man. It has created competition among observers, some of whom have dropped everything at the ring of a phone, and the outlay of substantial cash, to travel as many as several thousand miles to observe a new bird species (quite often a bird outside its normal range) and add it to their personal "Life" or "North American" list. Birdwatching's support of the automotive industry must be substantial. Under current guidelines, a birders "par" is broken when the observer has "listed" 600 or more of the 800 plus-or-minus species in North America. No one has set a similar "par" for the more than 8,000 bird species worldwide. This challenging game now has developed to a point where standards are being established that listers much meet in

order to authentically place a bird species on one's personal lists. However, the honor system still must prevail!

Among all these human pleasures derived from birds, far be it for me to assign any priority. Each is important in its own way to each individual human.

Profit

Many of the "pleasures" just covered, and those topics to follow under "pain" have profitable connotations.

Scientific Relations.--Certainly the role of birds as subjects of scientific research has proved profitable to mankind, not only in studies of individual and population behavior but in development of other knowledge such as natural selection. Fossil bird records have helped man understand earth's geological periods and environments therein. Birds eggs are useful in disease and reproduction studies. Birds have served as testers of air quality for humans in the trenches during World War I and in our deep coal mines, as well as indicators of broader environmental quality contexts stressed by Rachel Carson in "Silent Spring." Finally, birds undoubtedly played an important role as seed dispensers in the vegetating of newly-formed oceanic islands and other devegetated or un-vegetated areas.

Environmental Health.--Many birds serve in a beneficial manner as controllers of weeds, invertebrate and vertebrate pests detrimental to man and his established environments--their capabilities for disease and weed spread notwithstanding. Other birds perform as sanitary engineers in nature's scheme of things, and their role in scientific research related to human environmental quality leads to human health benefits.

In Commerce.--Birds have provided man with meat, egg and feather products. Nests of an Asiatic swift are used in soups. Guano deposits provide fertilizer used by man. Cormorants have been used to catch fish for humans in the Orient.

Commercial harvest of birds and/or their parts long was important economically, but trade in America today is fairly-well limited essentially to live birds used in research and in the pet trade. There is broader commerce elsewhere in the world. Many of what were commercially harvested species are now nongame birds, and some are even extinct, endangered or

threatened species.

Similarly, sport hunting of birds has meant big business for arms and ammunition manufacturers, land owners, the tourist trade and all the suppliers thereof. Further, support for much of professional wildlife resources management expenditures have derived from this same sport hunting of waterfowl, gallinaceous and shorebirds.

The average human's growing interest in birds has produced a booming business in birdseed, feeders, birdbath heaters, and nest boxes, and has brought forth a deluge of bird books and bird art on the market.

I referred earlier to the basic natural interest which most humans have for birds and other animals. There is no better evidence for this than in the market place where birds play an unusually prominent role on notepaper, stamps, pillows, jewelry, shirts and other clothing, mailboxes, household dishes and glassware, lampshades, bookends, and bric-a-brac. Even wastepaper baskets with a bird added to its design will bring a sales price of over \$10 instead of \$2 or less for a plain one! Such is profitable commerce with birds.

Pain

After all the favorable things I discussed under "pleasure," it may surprise some of you to learn that birds can involve "pain." You will recall that in introducing the three P's, Pleasure, Profit and Pain, I stated that "pain" also should embrace losses, damaging or harmful actions within consideration of bird and human relationships.

Disturbance and Disruption.--Actions that disturb or disrupt the normal flow or conduct of human activity are usually considered harmful. The perching, roosting, feeding, or nesting habits of birds may create such conditions. Nestings may preclude or delay use of traffic lights, machinery, moving of a piece of equipment, or even the pruning of a shrub, the felling of a tree or the moving of a field. Birds reaching home interiors through chimneys or other vents may create crises, and even dirty the furnishings. Nest debris may create fire or health hazards, and defecations at points of concentrated bird use may be dirty or slippery. Night singing, early morning calling and drilling on home rooftops may disturb the rest of humans.

Damages by Birds.--Several bird activities may be at least damaging, though not wholly destructive. Defacement of buildings by defe-

cation or sporadic drillings may necessitate repairs. Extra clothes cleaning bills and car washes add to one's living costs. The federal government grants a commercial contract preceding each presidential inaugural parade for the purpose of freeing the parade route and temporary seating facilities from urban bird concentrations just for such reasons. Even the White House grounds have a series of loud speakers installed over which special recordings of bird distress calls are played to discourage concentrations of roosting birds about the building and grounds.

At a Bethesda, Maryland church the architects created such an intricate exterior design motif that the pigeons and starlings are attracted to its shelter for perching and nesting. These birds sometimes make so much noise it is difficult to hear the pastor's sermon. Maybe that is the Lord's way, but it is certainly disturbing to church-goers, as well as resulting in building defacement. Among other damaging effects, birds are known to be important links in the distribution of Psittacosis and Salmonella, both detrimental to man.

Destruction by Birds.--Concentrations of birds at attractive roosting and feeding sites may be costly. Their presence may create hazards to aircraft and has resulted in the loss of human life when birds collided with aircraft. Similarly, roost concentrations have defoliated holly orchards, ruining them for commercial purposes, producing severe losses for the orchardists. Woodpecker drillings in telephone poles have disrupted line services and have necessitated costly replacement of the weakened poles. Similar drillings on wooden buildings have destroyed parts of the buildings. Man's agricultural monocultures have proved extremely attractive to vast hordes of grain-feeding birds that have at times seriously wiped out production of corn or other grains. Osprey take fish from fish farm and hatchery ponds, and other birds destroy vegetable garden crops.

Human Detriments to Birds.--Not all "pain" is caused to humans by birds. Contrarily, man's increasing population of earth is constantly reducing or altering most types of habitats available to birds, crowding them into less and less space, which often may be of a less desirable quality for the birds. Many of man's activities pollute the natural environment: chemicals in the air weaken or kill forest trees, and oil spills spread over marine and coastal waters taking their toll of birds. Other persistent pesticides placed in the environment by man are, through the natural processes of food chain functionings, concentrated to a lethal point in

those birds feeding near the top of the food chain. Man also takes his toll of birds through his physical structures such as large picture windows in homes and office buildings, through erection of tall transmission lines and towers, and through the planting of food plants attractive to birds in narrow median strips of super highways. High speed traffic takes a heavy toll of birds. On the other hand, buildings and bridges may provide ideal new habitat for birds.

IN SUMMARY

This has been an all-too-brief and sketchy review of many of the pros and cons about the interrelationships between humans and birds. It is hoped the ideas in this background review will be helpful to land managers who must not only understand the nongame birds and their habitats, but some of the intricacies of human interests and relationships to birds. With this understanding, successful management programs stand a better chance to be realized on America's diverse forest and range habitats.

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Recreation Development — A Case History of the Mile Hi Lodge¹

Carroll A. Peabody^{2/}

The purpose of this manuscript is to inform people of how and why the Mile Hi became the sanctuary it is today. The native plant life and weather conditions in Ramsey Canyon make this area a haven for many birds and other wildlife. Now it is man's responsibility to maintain and preserve areas such as this--for the sake of the birds and also for the enjoyment of nature lovers like ourselves.

I am, as the owner of the Mile Hi, thankful for the opportunity to present the Mile Hi story. Not only in the hope that it might encourage more recreational facilities of this type which are greatly needed, but that it also might encourage the Forest Service not only in utilizing more efficiently some of its holdings, but furnish ideas on encouraging better use of private inholding property.

Of course the thought has crossed my mind that in presenting this, some of those hearing of the Mile Hi for the first time might vacation with us--and in so doing, would increase our income and our list of friends.

It all started with the birds, which incidentally was how the National Audubon Society originally had its start.

In 1960, my wife and I purchased a small ranch called the Mile Hi!, located in Ramsey Canyon, which is a north eastern canyon of the Huachuca Mountains in Cochise County, Arizona (about 90 miles southeast of Tucson). It was and still is a private inholding being about 1½ miles above the Coronado National Forest boundary. Where the ranch is located, the canyon is quite narrow with a wonderful mountain stream winding toward the rolling prairies below. Growing along the stream are some of the largest and most beautiful Syc-

more trees found anywhere. These are intermingled with Big-tooth Maple, many varieties of live Oak, Pine and Juniper trees. In spite of an elevation of 5450 feet, a thermal current is ever present which protects the habitat and wildlife from extreme heat and cold.

Thanks to the previous owners for not having cleared the slopes of the natural growth, we also vowed never to cut trees or brush unless in extreme emergency, which to date has not occurred.

Just prior to our purchase, Mr. Crawford Greenwalt had spent considerable time at the Mile Hi! photographing hummingbirds. Many of his pictures were included in his now world-famous book entitled "Hummingbirds".

At the time we purchased the Mile Hi! there were a couple of well-built, but rough cabins which had been rented out to anyone that was willing to live there for the small fee of \$60 per month.

In 1961 a couple stopped in to watch and study hummingbirds. They took a cabin that was empty and at the end of their stay offered to pay \$7.50 per night! This was the turning point of the now famous Hummingbird Capitol of the U.S.A.--The Mile Hi!

We acquired, read, and studied all material we could get our hands on during the next few months concerning hummingbirds. By the following Spring, we had remodeled the cabins, become a bit more knowledgeable about hummingbirds, and we had put out many more feeders. Word was spreading that Ramsey Canyon was the place to visit if one wished to see a variety of hummingbirds.

¹ Paper presented at The Symposium on Management of Forest and Range Habitats for Non-game Birds, Tucson, Arizona, May 6-9, 1975.

² Owner, Mile Hi Lodge, Pres., Huachuca Audubon Society.

To date, 15 species of hummingbirds have been identified at the Mile Hi!, 14 of which have been photographed--this is in addition to a few hybrids that have been observed from time to time. By July and August every year, there are so many hummingbirds around that we use approximately 115 pounds of sugar per week.

We rented the cabins by day or by the week to those interested in the hummingbirds during the Spring and Summer. During the Fall and Winter, we rented the cabins to military personnel from nearby Ft. Huachuca. The extra income was used to build additional cottages. We now have six cabins in addition to the main ranch house. Because of the delicate ecological situation, we have decided against expanding further.

In 1966 we began to advertise in the National Audubon Magazine, and as a result more and more persons flocked to the Mile Hi to see the birds. By this time we were finding that hummingbirds were not the only birds around. Not only were many other species of birds identified during the Spring and Summer months, but we were also finding that winter birding was very rewarding. As a result, the Ramsey Canyon Xmas Count was initiated and 130-140 species are normally found during this time. Within the Xmas Count area--which is a 15 mile diameter circle including a 9300 ft. mountain peak in the Huachucas, wonderful slopes and riparian growth of at least 5 canyons in the Huachuca Mountains, and the grasslands between the mountain ranges and the San Pedro River--some 300 species of birds have been seen and identified.

Destruction of some of the nesting habitat of the Coppery-tailed Trogon and the very unusual Buff-breasted Flycatcher by Fort Huachuca authorities was influential in the formation of the Huachuca Audubon Society and its affiliation with the National Audubon Society. All of this has added to the popularity of the Mile Hi! among birdwatchers and naturalists, which keep our cottages full most of the time.

Only a few years ago birdwatching was hardly considered a form of recreation--in fact, many people who enjoyed birdwatching would hardly admit it out loud.

Today, many millions enjoy birdwatching and the number of persons indulging is growing rapidly. In fact, at the Mile Hi! we have over 4,000 visitors every year, most of them from out-of-state and quite a few are from Canada or Europe. Many have come without reservations and they stay in local motels

or some are camping out or "trailerling"--but they all come to see the birds.

This brings up the question of why has birdwatching become so popular. I will briefly give just a few of many reasons:

1. Nearly all ages can and do participate.
2. One can spend as little or as much time as he has available.
3. Birdwatching can be as strenuous or as non-strenuous as one wishes.
4. A very minimum of cash outlay is involved--Guide book and binoculars can cost as little as \$25. Or, one can expand into photography, where the sky can be the limit.
5. One can travel or stay at home or just visit a local park.
6. Birdwatching takes one outside and close to Nature.
7. There are no great trophies or awards--just self-satisfaction at sightings and sharing them with others.

Then you may ask why we feel the Mile Hi! has become so popular. I will list a few reasons we feel have been most important:

1. We have permitted Nature to have dominion and have managed the ground as little as possible. The result has been a near perfect habitat not only for the birds, but also for other forms of wildlife. The Mile Hi! was blessed with an almost unmanipulated riparian growth at the canyon's bottom along the stream bed. This is becoming harder and harder to find elsewhere in these days.
2. We have used no poison sprays or toxic chemicals--the result has been healthy bird food such as insects and seeds. This has encouraged both the bird population and their predators, which in turn has allowed Nature to seek its own balance.
3. Both the birds and predators and other wildlife are enjoyed by our guests. Some of these animals include the ring-tailed cat, bobcat, fox, raccoon, coati-mundi, wild turkey, deer, javelina, various lizards, etc.
4. Our guests seem to enjoy the peace and quiet. We ask any one disturbing this tranquility to leave at once. The few cases of this have been motorcyclists that have found the place. These are in no way compatible with birdwatching or nature studies.
5. The cottages are built to harmonize with nature and are just far enough apart that the occupants will not disturb one another.
6. The staying guests are aided in seeing the things that are of particular interest to them.

Due to the Forest Service practice of attempting to acquire private inholdings, the Patagonia District of the Coronado Forest is to be complimented in their foresight and for their efforts in having acquired private inholdings. These areas contain much of the great riparian growth in the Huachuca Mountains, which enables our many peripheral species of wildlife to have a place to live in the United States.

We feel that there are other locations in both Forest Service holdings and private inholdings that might be just as successful a location as the Mile Hi! We also feel that many areas of recreation are not compatible with each other, just as some forms of multiple use such as strip-mining and cattle-grazing are not compatible in the same geo-

graphic location. This presents a serious need for the Forest Service with the help of all recreationists--such as Fish and Game Department, motorcyclists, hikers, Audubon groups, ranchers, etc.-- to get together and set aside prescribed locations for various needs and uses. In many cases I am sure, numerous uses can be applied to a given area.

We also feel that some individuals with inholding property could be induced to use their property to the benefit of both the Forest Service and the recreationist, and at the same time furnish a service that would result in a net gain for the property owner. At any cost, a way must be found to save the great canyons of the Huachuca Mountains and their riparian growth.

Discussion

MR. PETERSON: Mr. DeGraaf, why did you omit transportation costs?

MR. DeGRAAF: I had no way to estimate travel expenses. Our extensive surveys are based on reports of manufacturers, et al. To estimate travel costs would require extensive interviews of participants. If I could anticipate one other question, poultry feeds were excluded because manufacturers can't identify the uses of such products.

MRS. CECHMANEK: Dr. DeGraaf, are you aware of all the Audubon members and naturalists who buy duck stamps to support programs, even though they do not hunt?

MR. DeGRAAF: Yes. Waterfowl hunters also spend a lot of money for feeding and habitat management that benefit nongame. Some give money with that objective in mind.

MR. JANTZEN: Dr. Gottschalk, did you attempt to separate consumptive and nonconsumptive users in your estimates? People may be consumptive users of wildlife resources, but also invest in bird seed and things of this nature, and enjoy some of the nonconsumptive uses.

DR. GOTTSCHALK: I did not separate it out on a number of participants basis. I did indicate the two uses are not mutually antagonistic. What we need is more research.

MR. JANTZEN: I asked the question because expansion of the figure may result in unrepresentative of what actually exists.

DR. GOTTSCHALK: Right, there was quite a bit of overlap.

MR. KINGSLEY: Has anyone suggested the possibility of putting a tax of one cent per pound or something on bird seed to support development of programs for nongame species?

MR. DeGRAAF: In Massachusetts, there are two bills in the House to develop sources of funding based upon taxes on products.

MR. JAHN: The Wildlife Management Institute did explore the subject. Essentially, we took a look at the State Fish and Wildlife Management, land management, and other agencies and the primary institutions that are training people in fish and wildlife work.

We wanted to examine how much time in terms of man hours and how much money was now being spent on nongame fish and wildlife activities. Likewise, we wanted to get some estimate of additional man years and dollars needed to strengthen their programs. We also explored potential new sources of funds that could help to meet the defined needs. This report was filed with the Council of Environmental Quality and Department of the Interior. It has been officially released in the last 10 days. If you are interested in a copy, I suggest that you write to Russell Peters, Chairman of the Council on Environmental Quality in Washington, D. C.

DR. GOTTSCHALK: I might comment specifically on the problems that have been interposed in the past, in attempting to identify particular sources at the federal level. Specifically, a tax on bird food would be a new tax on an agricultural product. The tax bases for the Pitman-Robinson and Dingle-Johnson Acts were already in existence. It was possible to merely to have it diverted to a special fund. In looking at the possibilities from the practical standpoint of getting legislation through the Congress, we have to recognize that agricultural interests would likely appose the tax. The Office of Management and Budget and most administrative managers are opposed to earmarking funds. The administrator--having been one myself, I know about this--likes to have the utmost freedom to administer his funds in whatever way he feels is best. Translated to the highest level of the government, the Office of Management and Budget takes a very hard antagonistic position on any earmarking. Several years ago we came to the conclusion that it wasn't practical to attempt to get a tax law through. It just never got started. Maybe the time has come.

MR. BEALER: Dr. Gottschalk, in your closing remarks you indicated that we would perhaps have to be somewhat covert when we approached nongame studies. Could you comment further on this?

DR. GOTTSCHALK: I certainly didn't want to suggest that we had to be covert. I intended to indicate only that it was going to be difficult to get support, financial support, for programs that are identified for these species. I think that it is going to continue to be difficult to get the kind of support for

these programs that we would like to see as compared with programs that deal with commodities that are in common commercial exchange. With that difficulty the best hope we have is to attempt to show that the management of nongame birds is part and parcel of a broader conservation program approach. Tied in this way we have a better chance to push it forward, support it all along the way.

MR. EVENDEN: The Wildlife Society and the International Association of Game, Fish, and Conservation Commissioners developed a model law for nongame funding, with the intent that this could be developed and pushed through the various State legislatures. This is being worked on and I just mentioned it as a point of needed support at the State levels.

MR. LENNARTZ: I understand a number of States

have experimented to some degree on the sale of special stamps to raise funds. Do you gentlemen have information on these programs and what the response has been?

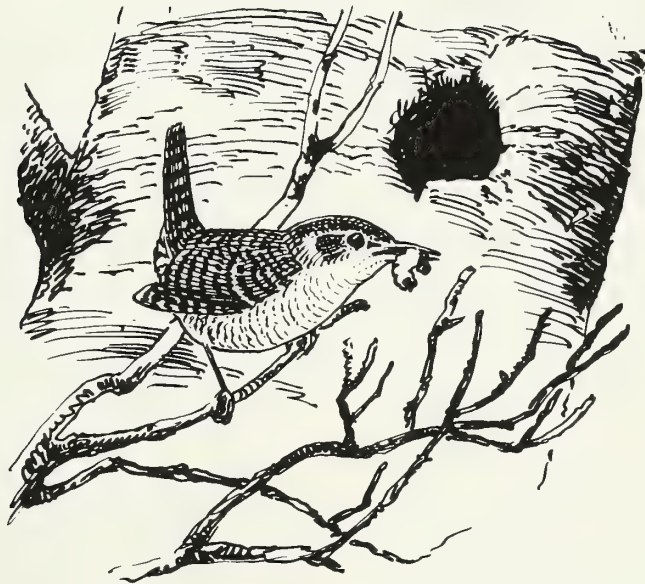
MR. EVENDEN: I have heard that the State of Ohio's program has not worked very well.

DR. GOTTSCHALK: There are now 14 States that have one form of funding or nongame wildlife or another. Perhaps the most successful has been the State of Washington. Granted that the expectations have not materialized, but they are still looking for something like \$200,000 a year from the personalized auto tags. The State of California has a plan under which funds are made available for nongame wildlife. In several other States, general funds are appropriated for nongame wildlife programs.

Tuesday Afternoon, May 6

Birds and Their Habitat

*Presiding: L. R. Jahn
Wildlife Management Institute*



Ecological Distribution of Breeding Birds¹

Steven R. Peterson^{2/}

Abstract.--The ecological distribution of breeding birds in the U.S. and southern Canada was analyzed using several diversity indices. Average species recorded per route and average species diversity indices calculated with the Shannon-Weiner function were lowest in the West and Southwest and highest in the forested areas of the East and Northeast. Significant differences were noted among strata but little difference was recorded among years. In the central U.S. and Canada, average species per route was positively correlated with latitude but the average species diversity index showed no significant correlation. Curves of cumulative species indicated additional species were still being recorded after 168 routes had been sampled. Cumulative species diversity index curves reached an asymptote after about 25 routes were sampled.

INTRODUCTION

Study of the ecological distribution of breeding birds in North America began when C. Hart Merriam, U.S. Biological Survey, developed the "life zone" concept in the early 1880s. Since that time, zoogeographers and ecologists have formulated more questions than answers as to why certain species or groups of species are restricted to particular habitats while other taxa are more ubiquitous in their requirements.

It is important to understand the relationship between similar and diverse avian communities (Bond 1957) but considerable difficulty arises when one attempts to analyze data that is largely intangible, inferential, or does not lend itself to proper testing (Kendeigh 1945). The lack of good quantitative

data on the relative numbers of breeding birds associated with the vegetation structure in various communities is apparent by its absence in the literature. It is difficult enough to obtain this information for a relatively small area, let alone a state, geographic region or continent.

Bird communities are readily influenced by plant succession (Odum 1945) and a more widespread appreciation of this concept would help many people interpret the appearance and disappearance of various species (Pitelka 1941). However, an understanding of succession, and the avifauna associated with each seral stage, also tells us that distribution data collected today will be obsolete tomorrow. Before I discuss our current analysis of the ecological distribution of breeding birds, I feel it is appropriate to briefly summarize the basic theories concerning avian ecogeography in North America.

The life zone concept purported by Merriam was developed from his observations on the San Francisco Mountains of Arizona. Merriam concluded animals were primarily restricted to six basic zones or transcontinental bands by temperature isotherms. These bands were designated as Arctic, Canadian, Hudsonian, Transition, Upper Austral, and Lower Austral. The life zone theory has been criticized by a number of people because the basic premise for the observed distribution was temperature. No doubt

^{1/} Paper presented at the Symposium on Management of Forest and Range Habitats for Non-game Birds, Tucson, Arizona, May 6-9, 1975.

^{2/} The data for this paper was collected while the author was a research biologist for the U.S. Fish and Wildlife Service stationed at the Migratory Bird and Habitat Research Laboratory, Laurel, Maryland. Present address: Assistant Professor, Department of Wildlife Resources, University of Idaho, Moscow, Idaho 83843.

temperature is important in avian distribution, but major areas of plant and animal life do not correlate well with it (Odum 1945). The zones may indicate groups of associated species with implied ecological significance (Pitelka 1941), especially in the Arctic and Canadian zones, but this association breaks down in the lower four zones (Odum 1945).

The biome theory for plant and animal distribution was developed a half century after the life zone concept (Clements and Shelford 1939). A biome is a major biotic community, such as Deciduous Forest or Grassland, and is characterized by specific "dominant" plants and "influential" animals (Odum 1945). The biome concept takes into account a number of limiting factors including temperature, climate, and cover. However, it is based on the potential or primitive site, and one must ask how realistic this is when, for example, the grassland biome has been modified so extensively by agriculture and grazing. Nevertheless, this concept has probably been one of the most productive in studying bird-vegetation relationships (Bond 1957).

Recently, the concept that has come into more widespread use is that of the biotic province. Udvardy (1963), for example, has divided North America into 17 ecogeographic faunal groups such as arctic, boreal forest, great basin, chaparral, etc. These ecological regions are similar in many respects to the biomes except they are generally smaller in area.

Each of these concepts involves an essentially artificial arbitrary division of the landscape for descriptive purposes (Bond 1957). Bond (*loc. cit.*) concluded that, in the deciduous forest at least, no discrete groups of bird communities were recognizable, but this continuum concept should not detract from delineating various groups as convenient working systems for description and analysis even though such groups be arbitrary.

Avian-vegetation relationships can be examined from two directions. Either the vegetation is divided into communities and the birds associated with this vegetative complex are determined, or else birds with similar ranges are grouped and the vegetation with which they are associated is recorded. Both methods are synthetic and involve the use of range maps developed from surveys or checklists. When species maps of birds with similar ranges are superimposed, they reveal centers of distribution for historically related groups having similar ecological requirements (Udvardy 1963). Unfortunately, many studies of this nature rely solely on range outlines and do not consider population density within these communities.

It has often been recorded that many species are more closely associated with the

vegetational life form or physical appearance of the habitat than with a particular plant species in the community. The many wood warblers in deciduous forests, spruce grouse in conifer forests, or prairie chickens in the tall grass prairie are good examples. In essence then, vegetation shape or structure, especially in climax situations, apparently represents what the birds are responding to (Bond 1957). Even though the range of a particular species or group of species may correspond well with the range of a particular life form or community, this association may be just coincidence in limits of tolerance or actually be due to some obligatory relationship (Kendeigh 1945). Species tolerances may be similar but they are never exactly the same, and the fact that groups of species occur together dictates studies of group behavior associated with major communities (Pitelka 1941).

METHODS

The Breeding Bird Survey conducted annually by the U.S. Fish and Wildlife Service, with the help of carefully selected amateur and professional ornithologists, provides a basis for making a quantitative, as well as a qualitative, analysis of breeding bird distribution. This survey was started in 1965 and since 1968 has encompassed the 48 contiguous states and southern Canada. The study was designed to help monitor environmental quality by measuring changes in abundance of North American breeding birds. Except for a few rare and local species, no adequate method had existed for measuring populations of non-game species on a continental basis. This survey not only provides a picture of species composition in different ecological strata but estimates of relative abundance as well.

The survey is essentially a stratified random sample of roadside habitats. Methodology and certain results have been presented previously by Robbins and Van Velzen (1967, 1969) and Van Velzen and Robbins (1971). The breeding bird survey, 1969. Administrative Report, U.S. Fish and Wildlife Service. 75pp.). It is based on all birds seen or heard within one-fourth mile (1 mi = 1.61 km) during fifty 3-minute stops spaced at half-mile intervals along randomly selected 24.5-mile routes. One-degree blocks of latitude and longitude were used as a basis for route selection to ensure good geographic distribution of the routes. Both starting point, as well as direction of travel for 1 to 16 routes within each block, were determined from a table of random numbers. The total area encompassed by the survey was divided into 56 ecological strata (fig. 1) according to a modification of the schemes

Figure 1.--Ecological strata for North America (Modified from Kuchler 1964 and Fenneman 1931, 1938).

Stratum Number	Stratum Name	Stratum Number	Stratum Name
1	Sub-tropical	34	High Plains Border
2	Floridian Section	35	Staked Plains - Pecos Valley
3	Lower Coastal Plain	36	High Plains
4	Upper Coastal Plain	37	Western Lake Section
5	Mississippi Alluvial Plain	38	Missouri Plateau - Glaciated
6	West Gulf Coastal Plain	39	Missouri Plateau - Unglaciated
7	Nueces Plain	53	Edwards Plateau
11	Piedmont	54	Colorado Plateau and Canyonland
12	Southern New England	61	Black Hills
13	Ridge and Valley	62	Southern Rocky Mountains
14	Highland Rim	63	High Plateaus of Utah
15	Lexington Plain	64	Central Rocky Mountains
16	Eastern Lake Section	65	Okanagan Highlands
17	Wisconsin Driftless Area	66	Sierra-Trinity Mountains
18	St. Lawrence Valley	67	Cascade Mountains
19	Ozark-Ouachita	68	Canadian Rockies
21	Cumberland Plateau	81	Mexican Highlands
22	Kanawha Plateau	82	Southern Sonoran Desert
23	Blue Ridge	83	Northern Sonoran Desert
24	Allegheny Plateau	84	Pinyon-Juniper Woodland
26	Adirondack Mountains	86	Wyoming Basin
27	Northern Hardwoods	88	Great Basin
28	Spruce-Hardwood Forest	89	Columbia Plateau
29	Closed Boreal Forest	91	Central Valley
30	Aspen-Parklands	92	Foothills
31	Till Plains	93	Southern Humid Coastal Belt
32	Dissected Till Plains	94	Northern Humid Coastal Belt
33	Osage Plains	95	Southern California Mountains



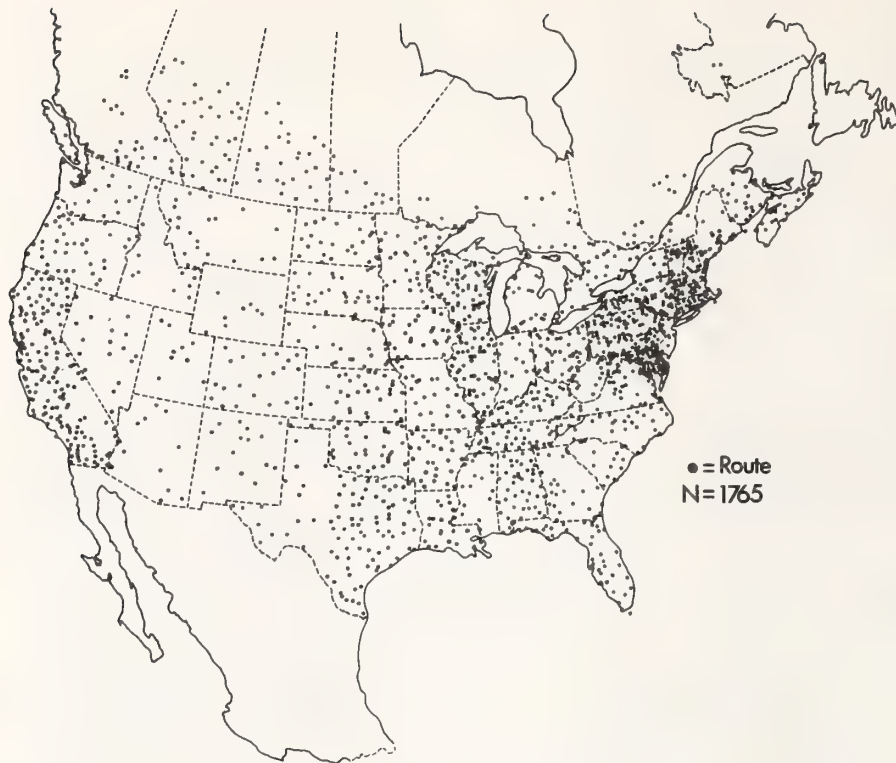


Figure 2.--Continental distribution of breeding bird survey routes. Only those routes run in 1973 are mapped.

presented by Küchler (1964) and Fenneman (1931, 1938). Each route was assigned to the stratum encompassing the route's coordinates. Field methods were carefully standardized and remained unchanged throughout the 6-year period of this report. Each observer started one-half hour before local sunrise and approximately 95 percent of the routes were completed during June.

For practical reasons, counting has to be limited to roadsides. Hence, the Breeding Bird Survey is a sample of roadside habitats and not of all habitats within a given stratum. Data collected from routes run in the Spruce-Hardwood Forest stratum, for example, should not be construed to mean birds were only recorded from Spruce-Hardwood Forest *per se*. On the contrary, many other small pieces of habitat are encountered along roads, including ponds, bogs, cultivated fields, cutover areas, urban developments, etc., and these different types of habitat are a part of that stratum as we have delineated it. These facts should be kept in mind when conclusions are drawn from the data presented. The continental distribution of all routes run in 1973 is presented in figure 2, while Table 1 indicates only those routes run between 1968 and 1973

that were used in analyses. About five percent of the routes run each year do not meet specified quality control criteria and are unacceptable for analysis. Hence, the total routes run in 1973 (1,765; fig. 2) is more than the total used for analysis (1,670; Table 1) in 1973.

The data were analyzed by calculating several different species diversity indices for each stratum. Many indices for calculating the species diversity of a community exist in the literature (Fisher et al. 1943; Shannon and Weaver 1963, original paper published 1949; Simpson 1949; Pielou 1966a,b; McIntosh 1967). Numerous investigators have attempted to evaluate and compare the various attributes of each index (Margalef 1958, Pielou 1967, McIntosh 1967, Hurlbert 1971). Different indices measure different aspects of the abundance between species (Hill 1973). In general, however, ecological diversity is at a minimum when all the individuals belong to one species, whereas diversity is at a maximum when every individual belongs to a different species.

The simplest index to diversity is the total species in a given area, or average number of species if more than one sample is taken. We selected average number of species

Table 1.--Routes sampled in each stratum from 1968 through 1973 and used in analyses.

Stratum	6-year average	1973	1972	1971	1970	1969	1968
Black Hills	1.8	2	1	2	2	2	2
High Plateaus of Utah	2.7	2	2	4	2	3	3
Sub-tropical	3.8	3	4	5	5	4	2
Okanagan Highlands	4.0	10	3	3	3	2	3
Canadian Rockies	4.2	3	1	4	6	6	5
Wyoming Basin	5.0	6	6	5	6	4	3
N. Humid Coastal Belt	5.2	13	3	3	5	4	3
Colo. Plat. & Canyonland	5.5	4	5	7	4	6	7
S. Rocky Mountains	5.5	8	6	6	6	4	3
N. Sonoran Desert	6.0	10	7	3	8	4	4
Pinyon-Juniper Woodland	6.2	7	7	6	6	5	6
S. Sonoran Desert	6.7	14	6	6	5	4	5
Staked Plains - Pecos Vly.	7.0	8	8	7	4	8	7
Cumberland Plateau	7.8	9	8	8	7	7	8
S. Calif. Mountains	8.0	10	9	10	9	2	--
Sierra-Trinity Mts.	8.8	20	17	7	5	2	2
St. Lawrence Valley	9.0	9	9	8	10	9	9
Blue Ridge	9.8	10	9	11	10	7	12
N. Hardwoods	10.0	13	12	13	7	9	6
Lexington Plain	11.0	10	11	12	10	10	13
Central Valley	11.8	20	24	9	8	4	6
Edwards Plateau	12.5	15	16	14	9	14	7
Nueces Plain	13.0	11	17	14	14	16	6
Adirondack Mts.	13.3	12	10	12	15	16	15
Mexican Highlands	13.7	14	12	15	13	15	13
Cascade Mountains	13.8	21	14	14	10	11	13
Aspen - Parklands	15.7	25	25	17	12	9	6
Closed Boreal Forest	16.3	29	19	19	14	10	7
Great Basin	16.3	22	19	16	14	14	13
Central Rocky Mountains	16.7	29	20	15	10	15	11
Floridian Section	16.8	18	18	18	17	15	15
High Plains Border	17.0	19	21	18	13	16	15
Columbia Plateau	18.7	28	30	19	10	12	13
Ozark - Ouachita	21.2	27	23	19	19	22	17
Miss. Alluvial Plain	21.5	23	22	21	21	20	22
Foothills	21.5	47	34	17	17	7	7
S. Humid Coastal Belt	22.0	34	34	21	18	13	12
High Plains	22.2	25	21	22	24	24	17
Wisconsin Driftless Area	24.0	27	26	25	25	23	18
Lower Coastal Plain	26.2	27	28	28	28	22	24
Missouri Plat.-Glaciated	26.3	33	33	28	28	20	16
Kanawha Plateau	31.7	42	36	31	32	29	20
Missouri Plat.-Unglac.	32.8	33	35	34	34	31	30
Highland Rim	38.0	39	39	39	37	38	36
West Lake Section	38.3	50	38	43	36	30	33
S. New England	39.0	53	41	40	36	33	31
Dissected Till Plains	40.2	42	42	40	37	40	40
Piedmont	43.5	52	40	42	44	41	42
Osage Plains	46.0	45	48	49	46	47	41
West Gulf Coastal Plain	46.7	54	49	51	47	43	36
Till Plains	52.3	67	61	60	43	42	41
Ridge and Valley	63.2	68	62	70	68	57	54
Allegheny Plateau	74.0	88	77	81	76	66	56
E. Lake Section	75.7	74	79	83	76	72	70
Upper Coastal Plain	117.2	118	126	118	121	116	104
Spruce-Hardwoods Forest	151.5	168	162	154	155	140	130
Continental Average	25.0	29.8	27.4	25.8	24.1	22.2	20.7

as one of our indices because it is a readily understood reflection of diversity and was easily retrieved from the file. Pianka (1966) indicates this index is probably adequate for detecting differences on a local or regional scale, especially when it is difficult to appraise species abundance. In this paper we use the average number of species as a measure of diversity in different strata even though we do not specifically refer to it as a diversity index.

The actual number of species is better replaced by an index called the "Bird Species Diversity" (MacArthur and MacArthur 1961) as it incorporates both the number and abundance of each species. The Shannon-Weiner function,

$$H' = -\sum_i p_i \log_2 p_i,$$

was developed for use in information theory (Shannon and Weaver 1963). In this formula p_i is the probability of occurrence in a set of possible events. Margalef (1958; English translation of paper originally presented in Spanish, 1957) promoted the use of this formula in the biological field, and MacArthur and MacArthur (1961) used it to calculate an index to breeding bird diversities. Several authors (Lloyd and Ghelardi 1964, Tramer 1969) have partitioned Shannon's formula into two parts: evenness - a measure of how evenly distributed the proportions of each species are; and richness - a measure of how many species there are in the population. By partitioning the data they examined which factor was exhibiting the greatest influence on the index. We elected to use:

$$H' = -\sum_{i=1}^S \frac{n_i}{N} \log_e \frac{n_i}{N}$$

where N is the total number of individual birds recorded on each Breeding Bird Survey route and $n_1 \dots n_s$ are the frequencies of species recorded. Whenever we use the term "species diversity index" in this paper, we are referring to calculations based on the Shannon-Weiner function.

In no area of reference is the actual size and species population known; therefore estimates of species diversity must be calculated based on samples from these areas. In our formula, what is estimated is Shannon's measure of information which is a function of the population proportions of the various species (Pielou 1966b). The diversity of our samples, as measured by H' , is dependent on three variables: a) total individuals, b) number of species, and c) relative abundance of species. The primary assumption, under which the index is normally calculated, is that the sample is large enough to include all the species, and in the same proportion in which these species occur in the population (Pielou

1966a).

Lloyd and Ghelardi (1964) concluded there were two ways of looking at the species diversity in a given area: a) all the species that are living together there now have a certain species diversity value (E), or b) there is some true average value (ϵ) for a given size sample, but (ϵ) and (E) are not necessarily the same. In this study, theoretically the basic sampling unit in each stratum would be the individual bird. Since the number of routes varied between strata and we did not know the number of species in the various strata sampled, we used H' to estimate (ϵ). That is, we calculated an average species diversity index per route in each stratum, then treated the data statistically to test for differences among strata and years.

Pielou (1966b) suggested combining data from successive samples to obtain cumulative species diversity indices. With a sufficiently large sample size from a finite population, the plotted data will assume a curve similar to the species-area curves in quadrat sampling of vegetation. We used this method to plot cumulative species diversity indices vs. cumulative number of routes to determine the sample size necessary to arrive at an index value where the curve has essentially flattened out. If the curve assumes an asymptote, we have an estimate of Lloyd and Ghelardi's (1964) value for (E), but our estimate may be slightly lower than the true population value if all the species are not included in the sample.

RESULTS

Ecological Stratification

Average Number of Species

The average number of species recorded per route was calculated for each year in the 56 strata. An overall 6-year mean was then computed and the strata arranged in ascending order by this mean to examine the data for apparent trends (Table 2). The overall average number of routes run in each of the 56 strata during the 6-year period was 25. On a strata basis the number of species recorded per route varied from 20 in the Colorado Plateaus and Canyonlands stratum to 63 in the Northern Hardwoods stratum, while the continental average was 46. An average of 20-35 species was recorded in desert areas of the West and Southwest, 35-50 were recorded through the prairie region, and 50-63 species were recorded on routes in the heavily wooded areas of the northeastern United States and southeastern Canada (Table 2). The three sections of the Rocky Mountains (southern, central, and Canadian) each contained about the same number

Table 2.--Average number of species observed per route over six years and fifty-six strata.

Stratum	6-year average	1973	1972	1971	1970	1969	1968
Colo. Plat. & Canyonland	20.1	20	21	18	19	23	20
N. Sonoran Desert	21.7	20	20	26	21	21	21
Great Basin	22.4	22	24	22	21	23	23
Staked Plains - Pecos Vly.	25.1	28	27	21	27	23	25
S. Sonoran Desert	25.6	25	25	24	24	23	32
Wyoming Basin	25.7	25	27	31	27	24	21
High Plateaus of Utah	27.6	27	23	25	31	28	31
Central Valley	29.7	31	30	30	27	30	31
Columbia Plateau	31.9	38	37	31	32	29	25
High Plains	32.7	32	32	33	33	33	32
Mexican Highlands	35.9	37	33	36	37	35	38
Edwards Plateau	36.3	39	37	34	36	36	35
Missouri Plat.-Unglac.	37.8	41	40	38	36	36	36
Pinyon-Juniper Woodland	38.2	40	35	39	37	42	36
Black Hills	38.3	41	39	39	37	39	35
Sub-tropical	40.1	35	40	43	40	41	41
Nueces Plain	42.3	43	43	40	43	43	42
N. Humid Coastal Belt	43.4	50	33	42	48	49	40
Foothills	44.1	47	46	43	43	44	42
S. Rocky Mountains	44.4	46	45	40	40	46	49
Osage Plains	44.6	45	45	44	45	44	44
Missouri Plat.-Glaciated	44.8	45	44	43	44	50	43
High Plains Border	45.5	45	45	45	45	48	45
Miss. Alluvial Plain	45.8	47	48	46	44	46	43
Dissected Till Plains	45.9	46	47	46	46	44	46
Canadian Rockies	46.2	44	49	46	47	50	41
West Gulf Coastal Plain	46.3	47	47	46	48	43	46
Central Rocky Mountains	47.5	48	49	47	49	45	47
Till Plains	48.7	48	48	48	49	50	49
Cascade Mountains	48.9	51	53	46	51	51	41
Floridian Section	49.1	50	49	49	49	49	49
W. Lake Section	49.5	52	53	49	48	49	46
Lower Coastal Plain	51.3	53	52	52	50	51	49
Closed Boreal Forest	51.5	48	48	54	53	54	51
Piedmont	51.3	53	51	52	51	51	51
Upper Coastal Plain	51.7	53	53	53	51	50	52
S. Calif. Mountains	52.1	48	54	49	50	59	--
Okanagan Highlands	53.0	55	63	52	48	43	58
Aspen - Parklands	53.3	53	55	57	54	53	48
Sierra-Trinity Mts.	52.4	50	47	53	53	57	56
Blue Ridge	53.4	54	55	53	52	52	54
S. Humid Coastal Belt	54.0	57	54	50	56	53	54
E. Lake Section	54.4	56	55	55	54	53	52
Ozark - Ouachita	54.5	54	54	54	57	54	55
Allegheny Plateau	54.9	55	56	56	53	54	55
Ridge and Valley	55.0	54	55	55	55	56	55
S. New England	55.8	56	56	56	54	56	56
Kanawha Plateau	55.9	57	57	57	56	55	53
St. Lawrence Valley	55.9	58	58	58	57	55	50
Lexington Plain	56.4	58	56	56	55	56	58
Highland Rim	57.8	59	59	58	57	56	58
Cumberland Plateau	57.9	60	60	58	59	55	56
Wisconsin Driftless Area	58.1	58	59	59	60	57	56
Spruce-Hardwoods Forest	60.3	61	61	61	60	60	58
Adirondack Mts.	61.3	60	64	63	63	59	59
N. Hardwoods	63.3	62	63	59	68	65	63
Continental Average	45.56	46.1	46.0	45.4	45.6	45.5	44.7

of species (44, 47, and 46, respectively).

A two-way analysis of variance was used to test for statistically significant differences in the average number of species recorded per route between the 56 ecological strata, the 6 years, and the interaction between strata and years. The analysis was performed on the unweighted means in Table 2. Since sample size varied between strata and years, some of these means are better estimates of their population means than others. A very large F ratio for strata indicates a highly significant ($P < .001$) difference in the average number of species recorded per route between the various strata. The stratum means were not subjected to further analysis by one of the multiple range tests because of unequal sample sizes, but a few independent t tests were performed on these data to form some idea of the sample size required to get significance between two strata. For example, in 1973 an average of 20.4 species was recorded on the 10 routes run in the Northern Sonoran Desert and 25.1 species were recorded, on the average, over 14 routes run in the Southern Sonoran Desert. The difference of 4.7 species per route was not significant ($P > .1$). During the same year, an average of 45.8 species was recorded on 42 routes run in the Dissected Till Plains area of Iowa, Missouri and Nebraska, while 52.1 species were recorded, on the average, over 50 routes run in the Western Lake Section to the north. This difference of 6.3 species per route was significant ($P < .01$).

Table 3 suggests a significant difference in the average number of species observed per route over the 6-year period ($.05 \leq P \leq .01$ levels). An examination of the overall yearly means indicates a slight increase from 44.68 species per route in 1968 to 46.14 species per route in 1973. Even though a few species are known to be increasing their range (e.g., cattle egret, *Bubulcus ibis*; tufted titmouse, *Parus bicolor*; house finch, *Carpodacus mexicanus*) and could, therefore, be recorded on more routes each year, it is doubtful that the data would show a significant yearly increase due to these few species. The authors suspect the efficiency of the observers has gone up slightly over the years, however, especially since many observers run the same route year after year. Because rare species tend to be remembered, a previous encounter at a particular stop could influence the recorder to search more intensely where it was previously observed.

The interaction between strata and years was not significant ($P > .05$) and suggested no relationship between these factors. That is, the relative relationship of one stratum to another in the ranking did not change significantly from one year to the next, or, in another sense, strata relatively poor in species tend to remain low in the ranking year

after year, whereas strata rich in species tend to occur high in the ranking each year.

Species Diversity Index

Annual mean species diversity indices were computed for each stratum and these data were then ranked in ascending order (Table 3) for examination similar to the average number of species observed per route presented in Table 2. Among strata, the average diversity index for the 6-year period ranged from 2.063 in the Southern Sonoran Desert to 3.580 in the Cumberland Plateau area. Examination of Table 3 shows a ranking of the strata by species diversity indices very similar to the ranking of the strata by average number of species (Table 2). The desert areas of the West and Southwest still occur low on the scale while the Spruce-Hardwood Forest, Adirondack Mountains, and Northern Hardwoods of the Northeast are still high on the scale.

A few strata moved farther up or down the scale but most strata retained about the same position in the ranking. The Till Plains of Illinois, Indiana, and Ohio (the heavily cultivated eastern tip of the prairie wedge), for example, moved from twenty-ninth place in the average species ranking to twelfth place in the species diversity index (a drop in the ranking indicates a lower index value). This illustrates that the agricultural area has a moderate number of breeding species present but the avifauna is dominated by a few species. In fact, of all the individuals recorded in this stratum during 1973, almost half (48%) were of three species: house sparrow (*Passer domesticus*), red-winged blackbird (*Agelaius phoeniceus*), and common grackle (*Quiscalus quiscula*). The predominance of a relatively few species causes the stratum to have a relatively low species diversity index. Similarly, the Wisconsin Driftless Area had a relatively high average species per route (ranked 53 of 56) but the area is dominated by the same three species as above (38% of total individuals recorded) so that the ranking in the species diversity index went down to thirty-first.

A two-way analysis of variance was performed on the unweighted species diversity index means in Table 3. Again, we found a highly significant difference ($P < .001$) among the 56 strata and no significant differences ($P > .05$) between the 6 years or the interaction between strata and years. These values, as well as those from the analysis performed on the average number of species observed per route, indicate most of the variability in these data is associated with differences among strata. Analyses of data failed to show any significant annual changes in the indices, and the relationship of the number of species and

Table 3.--Average species diversity index per route for six years and fifty-six strata.

Stratum	6-year average	1973	1972	1971	1970	1969	1968
S. Sonoran Desert	2.063	1.96	1.89	2.03	2.24	2.01	2.26
Staked Plains -Pecos Vly.	2.090	2.13	1.99	1.92	2.33	2.07	2.10
Great Basin	2.105	2.17	2.14	2.11	2.07	2.10	2.04
Wyoming Basin	2.235	2.10	2.23	2.65	2.28	2.01	2.14
Central Valley	2.252	2.17	2.27	2.29	2.17	2.31	2.30
Colo. Plat. & Canyonland	2.282	2.31	2.32	2.20	2.18	2.46	2.22
N. Sonoran Desert	2.332	2.09	2.27	2.67	2.23	2.32	2.43
Missouri Plat.-Unglac.	2.383	2.53	2.46	2.42	2.35	2.27	2.28
Columbia Plateau	2.395	2.61	2.59	2.29	2.33	2.35	2.20
High Plains	2.397	2.38	2.40	2.46	2.44	2.39	2.31
High Plateaus of Utah	2.618	2.46	2.47	2.59	2.80	2.68	2.71
Till Plains	2.722	2.74	2.69	2.72	2.67	2.77	2.74
Missouri Plat.-Glaciated	2.752	2.80	2.79	2.74	2.66	2.83	2.69
Nueces Plain	2.755	2.61	2.75	2.69	2.77	2.80	2.92
Mexican Highlands	2.758	2.85	2.64	2.77	2.82	2.72	2.75
Pinyon-Juniper Woodland	2.765	2.87	2.65	2.87	2.74	2.72	2.75
Miss. Alluvial Plain	2.810	2.83	2.85	2.84	2.75	2.81	2.79
Edwards Plateau	2.815	2.83	2.80	2.75	2.84	2.82	2.85
Sub-tropical	2.860	2.71	2.89	2.87	2.93	2.87	2.90
High Plains Border	2.880	2.85	2.84	2.81	2.88	2.95	2.95
Dissected Till Plains	2.915	2.89	2.91	2.93	2.94	2.88	2.94
Foothills	2.932	3.04	3.05	2.96	2.93	2.93	2.70
E. Lake Section	2.938	2.95	2.94	2.96	2.95	2.91	2.93
Black Hills	2.938	2.99	2.95	2.99	2.95	2.99	2.77
Osage Plains	2.970	2.97	2.94	2.97	2.99	2.95	3.01
W. Lake Section	3.007	3.04	3.09	3.01	3.00	2.95	2.95
West Gulf Coastal Plain	3.048	3.03	3.04	3.00	3.15	3.01	3.06
St. Lawrence Valley	3.063	3.16	3.06	3.15	3.10	2.93	2.98
Canadian Rockies	3.103	2.82	3.34	3.11	3.20	3.14	3.01
Central Rocky Mountains	3.108	3.07	3.04	3.12	3.30	3.02	3.11
Wisconsin Driftless Area	3.123	3.11	3.16	3.16	3.14	3.06	3.11
Piedmont	3.123	3.17	3.10	3.11	3.09	3.09	3.18
N. Humid Coastal Belt	3.128	3.19	3.83	2.64	3.13	3.11	2.87
Allegheny Plateau	3.135	3.16	3.17	3.19	3.09	3.12	3.08
Floridian Section	3.138	3.15	3.11	3.14	3.14	3.12	3.17
S. Rocky Mountains	3.148	3.15	3.16	2.99	3.07	3.23	3.29
Upper Coastal Plain	3.157	3.21	3.19	3.17	3.13	3.12	3.13
Lexington Plain	3.158	3.13	3.19	3.16	3.18	3.17	3.13
Cascade Mountains	3.165	3.25	3.29	3.10	3.16	3.18	3.01
Ridge and Valley	3.173	3.20	3.18	3.18	3.15	3.20	3.13
Lower Coastal Plain	3.242	3.30	3.27	3.28	3.21	3.20	3.19
Okanagan Highlands	3.247	3.28	3.50	3.21	3.09	3.03	3.37
Aspen -Parklands	3.252	3.20	3.29	3.32	3.29	3.32	3.09
Closed Boreal Forest	3.262	3.19	3.15	3.32	3.31	3.37	3.23
Highland Rim	3.277	3.22	3.26	3.27	3.29	3.29	3.33
Kanawha Plateau	3.282	3.33	3.33	3.31	3.29	3.21	3.23
S. Calif. Mountains	3.292	3.24	3.29	3.26	3.26	3.41	--
S. New England	3.303	3.32	3.34	3.33	3.26	3.29	3.29
S. Humid Coastal Belt	3.315	3.32	3.33	3.28	3.34	3.30	3.32
Sierra-Trinity Mts.	3.327	3.23	3.20	3.36	3.34	3.28	3.55
Blue Ridge	3.348	3.33	3.44	3.21	3.29	3.42	3.40
Spruce-Hardwoods Forest	3.377	3.39	3.38	3.39	3.36	3.38	3.36
Ozark -Ouachita	3.417	3.39	3.35	3.39	3.49	3.45	3.43
Adirondack Mts.	3.457	3.44	3.49	3.44	3.49	3.42	3.46
N. Hardwoods	3.508	3.46	3.50	3.44	3.62	3.55	3.49
Cumberland Plateau	3.580	3.59	3.61	3.59	3.65	3.51	3.53
Continental Average	2.950	2.95	2.97	2.95	2.96	2.94	2.94

their relative abundances between strata does not appear to change from year to year.

It is also of interest to examine the year-to-year variability in the average species diversity index for the strata. Those strata with few routes run, e.g., Wyoming Basin (5.0 routes/year) or Colorado Plateaus and Canyonlands (5.5 routes/year), have a relatively large variance in their indices while strata with an average of over 50 routes run (e.g., Eastern Lake Section, Upper Coastal Plain, Spruce-Hardwood Forest) have relatively little variability. The continental averages for the 6 years varied from 2.94 to 2.97. A comparison of Tables 1, 2, and 3 indicates that strata with a low species diversity index also had few species recorded, but fewer routes were run as well. A correlation of species diversity indices with numbers of species indicates a strong relationship ($P < .001$), and a correlation of number of routes with average total species observed in the stratum also shows a strong relationship ($P < .001$). Even though the Breeding Bird Survey routes were the same length in all cases, we tested the null hypothesis that the average species diversity index in a stratum was not related to the number of routes. We performed two tests.

First, we computed a single species diversity index for each stratum by combining the species and individuals from all the routes run within each stratum for each year (Table 4). Then a 6-year average species diversity index was correlated with the 6-year average for the number of routes run in the stratum. No significant relationship ($P > .1$) between the number of routes and the overall species diversity index for the stratum was indicated.

Second, we selected a random sample of 10 species diversity indices from all strata that had at least 10 routes run in each of the 6 years. This selection gave us a balanced design for a two-way analysis of variance on 31 strata and 6 years with 10 replications. A high F ratio for strata also indicated a significant difference ($P < .001$) between the 31 selected strata. The low F ratio for years indicated nonsignificant ($P > .05$) results similar to what we found on the original samples. A Spearman's Rank Order Correlation between the original stratum mean and the selected sample mean showed a highly significant correlation ($P < .001$). This indicates the ranking had not changed when the samples of 10 were selected from the 31 strata and sample size did not significantly affect the average species diversity index in strata.

Latitudinal Stratification

We also examined the data for latitudinal gradients. Tables 2 and 3 suggest an increas-

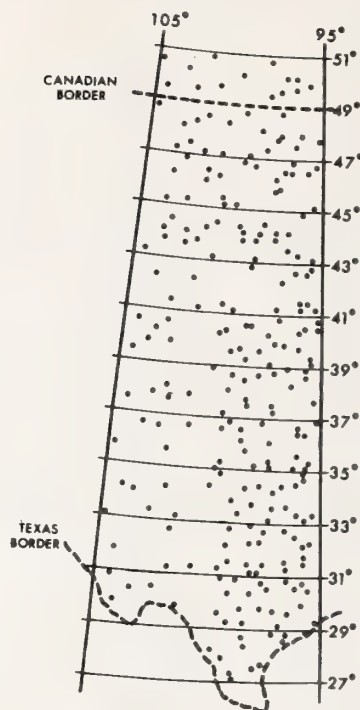


Figure 3.--Distribution of breeding bird survey routes by 2° latitudinal blocks in the central United States and Canada. Only those routes run in 1973 are mapped.

ing trend in average number of species and species diversity indices from the Southwest to the Northeast, but large physiographic differences occur within this region. To keep the physiographic changes to a minimum, we selected only those routes run between 95° and 105° West longitude (fig. 3). This is essentially the prairie country between the Rocky Mountains and the Mississippi River. We arbitrarily divided these longitudes into 2° latitudinal bands to give us an average of 18.5 routes run each year in each of the 12 bands.

Figures 4 and 5 illustrate correlations between the average numbers of species recorded per route and the average species diversity index per route with latitude in the prairie section of central United States and southern Canada. A positive relationship was found between numbers of species and degrees latitude north from southern Texas into Ontario and Manitoba ($P < .01$). However, no significant relationship was found between the species diversity index and degrees latitude south to north ($P > .1$).

Table 4.--Species diversity index calculated from all individuals, species, and routes run each year for six years and fifty-six strata.

Stratum	6-year average	1973	1972	1971	1970	1969	1968
S. Sonoran Desert	2.146	2.05	1.91	1.99	2.83	1.85	2.26
Staked Plains - Pecos Vly.	2.615	2.73	2.54	2.45	2.80	2.57	2.59
Central Valley	2.772	2.74	2.91	2.75	2.77	2.69	2.78
N. Sonoran Desert	2.852	2.71	2.89	2.93	2.99	2.74	2.85
Wyoming Basin	2.889	2.65	3.05	3.04	3.15	2.80	2.68
Missouri Plat.-Unglac.	2.901	3.09	3.03	2.96	2.82	2.73	2.77
Till Plains	2.924	2.96	2.88	2.93	2.88	2.95	2.94
High Plains	2.993	2.89	2.96	3.04	3.06	2.96	3.04
Black Hills	3.031	3.09	2.94	3.09	3.06	3.16	2.85
Colo. Plat. & Canyonland	3.043	2.87	2.97	3.15	2.89	3.31	3.07
Miss. Alluvial Plain	3.149	3.21	3.15	3.15	3.06	3.13	3.19
Edwards Plateau	3.175	3.20	3.18	3.11	3.06	3.23	3.26
High Plateaus of Utah	3.214	3.06	2.98	3.27	3.18	3.30	3.50
Nueces Plain	3.228	3.07	3.21	3.27	3.31	3.18	3.33
E. Lake Section	3.232	3.24	3.21	3.25	3.23	3.22	3.25
Dissected Till Plains	3.241	3.23	3.25	3.27	3.25	3.19	3.25
St. Lawrence Valley	3.292	3.34	3.26	3.38	3.33	3.17	3.27
Great Basin	3.331	3.44	3.39	3.35	3.27	3.23	3.30
Lexington Plain	3.350	3.32	3.39	3.33	3.37	3.38	3.31
High Plains Border	3.356	3.34	3.28	3.30	3.33	3.42	3.47
Piedmont	3.395	3.45	3.37	3.36	3.37	3.35	3.47
Allegheny Plateau	3.397	3.45	3.44	3.46	3.35	3.35	3.32
Sub-tropical	3.398	3.22	3.46	3.55	3.55	3.42	3.19
Wisconsin Driftless Area	3.401	3.34	3.45	3.46	3.42	3.33	3.40
Missouri Plat.-Glaciated	3.451	3.51	3.58	3.52	3.42	3.40	3.27
Columbia Plateau	3.458	3.72	3.68	3.39	3.35	3.43	3.19
Highland Rim	3.461	3.37	3.43	3.48	3.45	3.50	3.52
Canadian Rockies	3.487	3.11	3.33	3.53	3.76	3.60	3.58
Osage Plains	3.510	3.48	3.48	3.54	3.53	3.49	3.55
Floridian Section	3.520	3.49	3.50	3.48	3.57	3.51	3.57
Ridge and Valley	3.525	3.59	3.55	3.53	3.48	3.54	3.46
N. Humid Coastal Belt	3.525	3.77	3.34	3.47	3.59	3.55	3.44
Foothills	3.551	3.69	3.65	3.59	3.69	3.51	3.17
Pinyon-Juniper Woodland	3.567	3.60	3.45	3.53	3.56	3.65	3.61
Kanawha Plateau	3.593	3.61	3.61	3.61	3.62	3.57	3.55
W. Lake Section	3.619	3.66	3.71	3.63	3.61	3.56	3.55
S. New England	3.634	3.61	3.69	3.65	3.63	3.61	3.61
Upper Coastal Plain	3.640	3.66	3.67	3.64	3.62	3.59	3.66
S. Rocky Mountains	3.641	3.77	3.68	3.47	3.59	3.74	3.59
West Gulf Coastal Plain	3.686	3.75	3.66	3.64	3.75	3.64	3.68
Mexican Highlands	3.689	3.69	3.52	3.67	3.77	3.71	3.77
Blue Ridge	3.737	3.74	3.83	3.56	3.67	3.84	3.78
Lower Coastal Plain	3.791	3.88	3.81	3.82	3.76	3.73	3.74
N. Hardwoods	3.799	3.96	3.97	3.91	3.92	3.95	3.82
Okanagan Highlands	3.807	3.90	3.90	3.81	3.77	3.53	3.92
Ozark - Ouachita	3.835	3.80	3.75	3.83	3.89	3.89	3.85
Aspen - Parklands	3.839	3.84	3.90	3.86	3.86	3.81	3.76
Cumberland Plateau	3.843	3.88	3.89	3.88	3.89	3.78	3.74
Adirondack Mts.	3.848	3.84	3.85	3.87	3.86	3.83	3.83
S. Calif. Mountains	3.870	3.96	3.93	3.90	3.91	3.66	--
Sierra-Trinity Mts.	3.918	4.07	4.10	4.05	4.05	3.56	3.68
Central Rocky Mountains	3.987	4.07	3.93	3.94	4.05	3.98	3.95
Closed Boreal Forest	4.019	4.21	4.12	4.00	3.92	3.96	3.90
Spruce-Hardwoods Forest	4.063	4.07	4.09	4.11	4.05	4.02	4.04
S. Humid Coastal Belt	4.113	4.16	4.20	4.04	4.11	4.12	4.05
Cascade Mountains	4.192	4.32	4.27	4.12	4.18	4.19	4.08
Continental Average	3.456	3.53	3.47	3.46	3.49	3.43	3.42

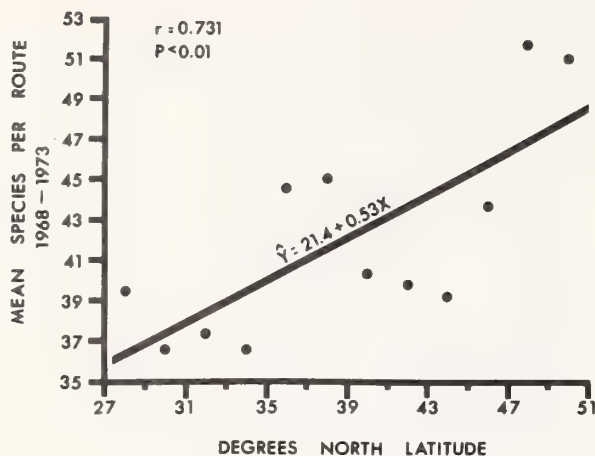


Figure 4.--Relationships of average number of species recorded per route with degrees north latitude between longitudes 95°00' and 105°00' West.

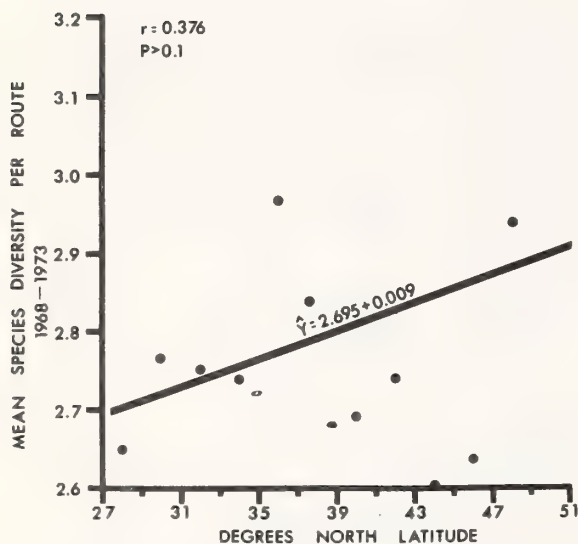


Figure 5.--Relationship of average species diversity recorded per route with degrees north latitude between longitudes 95°00' and 105°00' West.

Cumulative Indices

Another relationship we examined was developed by selecting a route at random from a particular stratum, then progressively adding data from each route in that stratum similar to the way species-area curves are developed

in vegetation studies. First, we compared total species in the strata by accumulating species, one route at a time (fig. 6). Next, we calculated cumulative species diversity indices by progressively adding the species and numbers of individuals, then recalculating the species diversity index from the pooled routes in each stratum (fig. 7).

Theoretically, if one kept increasing the sample size in a given stratum, he should eventually encounter all the species in that stratum. Figure 6 indicates that, even for the five strata with the most routes run in 1973, the slope of the cumulative species curve is still positive. For example, in the Spruce-Hardwood Forest stratum, 168 routes were run

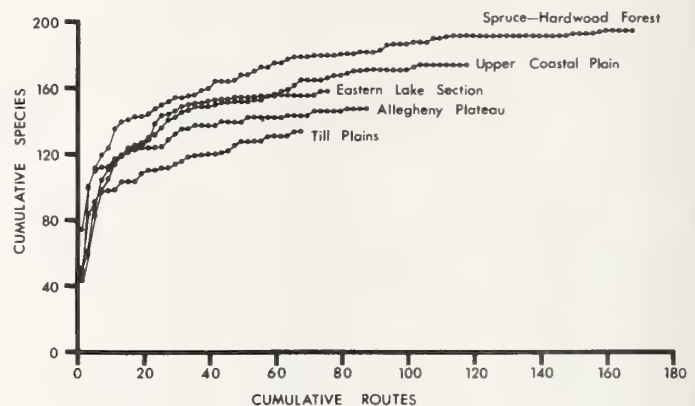


Figure 6.--The cumulative species observed in five strata during 1973. Data for every other route plotted.

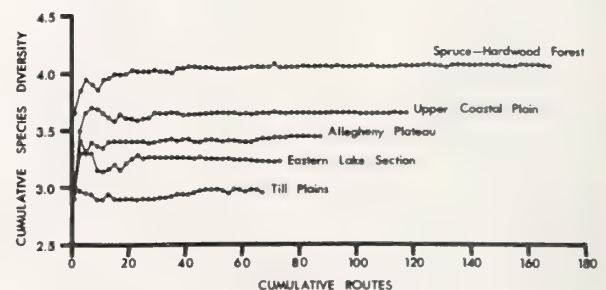


Figure 7.--The cumulative species diversity for five strata in 1973. Data for every other route plotted.

in 1973 and a total of 196 species was recorded. We do not know how many species bred in that stratum during 1973 but surely it was over 200. However, from the plot of our data, it was probably not over 250. After half of the routes (84) had been selected at random from the data, 177 (90%) of the total species recorded had been encountered. We have checked other strata and the curve for cumulative species appears to behave in a similar manner. Table 5 gives the total species recorded in all strata for the period 1968-73. The data have been arranged in ascending order by the 6-year average. In light of the curves presented in figure 6, one must be cautious in interpreting the ranking presented in Table 5. For those strata with relatively small sample sizes (e.g., less than 20; refer to Table 1) one might expect the total species to be on the lower end of the curve where it has a strong slope, but as sample size is increased, a higher proportion of the species will probably have been recorded.

A plot of the cumulative species diversity index for the five strata with the most routes run in 1973 (fig. 7) indicates this index reaches an asymptote much faster than the cumulative species index (fig. 6). After the data for 20 routes have been accumulated, the index changes very little. Each stratum has its own asymptote for the species diversity index and this is an estimate of (E), the overall species diversity index given by Lloyd and Ghelardi (1964). Overall species diversity indices for each year in all strata were presented in Table 4. Again, in light of the curves exhibited in figure 7, caution must be used in interpreting data from strata with few routes. For those strata with less than 10 routes, a doubling of the number of routes could change the overall species diversity index considerably, but if the stratum already has 20 routes, an increase in the number of routes would probably not affect this index very much.

DISCUSSION

Hill (1973) noted statistics such as the total number of species or species diversity indices are strongly affected by rarities and sample size. This is apparent in our data. While the size of the index is a function of sample size, the diversity of a community is a function of a number of variables including stability (MacArthur 1955), rigorousness, available niches, and energy flow (Connell and Orias 1964).

Bird species diversity is closely related to habitat diversity (MacArthur 1965) and habitats with similar profiles exhibit similar species diversity indices (MacArthur and

MacArthur 1961). Although our routes generally did not sample homogeneous stands of vegetation, as most investigators do when calculating diversity indices, nevertheless, the data can be meaningfully grouped by physiographic regions that, broadly speaking, have a similar type of vegetation structure or complexity. The dry relatively simple desert communities occur together; the prairie, brushy, and cultivated areas of the central United States group together; and the much more complex wooded areas, occurring primarily in the East, also group together. Intuitively, this is what one would expect, and numerous studies by MacArthur and his co-workers are good examples (MacArthur 1964, 1965; MacArthur and MacArthur 1961; MacArthur et al. 1966).

For a given profile, such as forested areas, the species diversity will vary with the complexity of that particular profile. For example, the diversity index for the Cumberland Plateau stratum was higher than the Spruce-Hardwood Forest stratum which was in turn higher than the Closed Boreal Forest. Likewise, the prairie pothole country of western Minnesota and the eastern Dakotas with its mixture of water, prairie, and cultivated fields had higher diversity indices than the heavily cultivated areas of the Till Plains stratum through Iowa, Illinois, and Indiana.

Mountainous regions in the United States exhibit a unique ecological (or environmental) complexity and their diversity indices are relatively high. All mountainous areas including the Appalachians, the Adirondacks, the Sierra-Trinity Mountains, the Southern California Mountains and the Cascades, as well as the three main parts of the Rockies, had relatively high diversity indices. This is partially due to our definition of the area, and the size of our routes. In addition, a physiographic unit of mountainous areas with considerable topographic and altitudinal relief has a complexity dependent upon several different major zones of vegetation compressed into a relatively small area. Cook (1969) found that areas with increased relief tended to be more complex ecologically and supported more species. When a 24.5-mile Breeding Bird Survey route is run across a mountainous area, many of these different habitat zones could be encountered. Consequently, many different species with relatively few individuals each will be recorded in each zone and this phenomenon probably gives us high diversity indices for these areas. If routes could be run solely within a given mountain zone we would expect to record diversity indices similar to their counterparts at other latitudes on the continent. However, in the United States it is virtually impossible to find 24.5 miles of accessible road in the alpine zone, for example, during June.

Table 5.--Total species observed in each stratum.

Stratum	6-year average	1973	1972	1971	1970	1969	1968
Black Hills	47.7	50	39	49	49	53	46
N. Sonoran Desert	54.5	71	59	51	64	42	40
High Plateaus of Utah	55.5	47	40	66	47	63	70
Colo. Plat. & Canyonland	57.0	54	52	62	45	66	63
Wyoming Basin	63.2	66	73	66	72	57	45
S. Sonoran Desert	65.2	82	67	59	55	54	74
Staked Plains - Pecos Vly.	66.0	69	77	61	59	62	68
Central Valley	75.3	98	98	74	62	54	66
Sub-tropical	76.2	62	78	94	81	82	60
Canadian Rockies	81.7	74	49	89	97	98	83
N. Humid Coastal Belt	86.2	112	62	83	92	87	81
Cumberland Plateau	87.2	91	91	87	87	84	83
Edwards Plateau	88.3	94	96	89	80	92	79
Lexington Plain	89.7	89	93	87	86	90	93
Okanagan Highlands	95.0	125	97	91	92	68	97
S. Rocky Mountains	96.0	111	100	94	95	91	85
Blue Ridge	100.8	102	108	103	97	94	101
Pinyon-Juniper Woodland	101.0	113	91	96	102	107	97
Great Basin	102.5	118	118	96	87	98	98
Nueces Plain	105.7	100	111	109	119	118	77
Miss. Alluvial Plain	105.7	109	107	105	103	105	105
S. Calif. Mountains	106.2	113	116	113	107	82	--
Ozark - Ouachita	106.8	113	106	108	103	103	108
Floridian Section	107.8	109	102	109	106	111	110
St. Lawrence Valley	109.3	111	113	108	114	109	101
Highland Rim	111.0	111	115	112	113	106	109
High Plains Border	113.8	118	116	108	106	126	109
Kanawha Plateau	114.0	119	115	113	115	113	109
High Plains	115.3	122	115	108	121	121	105
Sierra-Trinity Mts.	115.8	146	144	127	122	81	75
Adirondack Mts.	117.7	113	119	119	123	120	112
Dissected Till Plains	118.8	127	117	122	115	120	112
Wisconsin Driftless Area	120.5	129	119	124	125	117	109
Piedmont	121.0	129	125	118	121	120	113
Lower Coastal Plain	123.7	123	122	135	120	120	122
N. Hardwoods	124.0	136	131	126	119	123	109
Till Plains	126.2	133	125	125	120	127	127
Columbia Plateau	127.0	158	160	123	107	115	99
Foothills	127.5	177	153	122	126	97	90
Osage Plains	129.8	131	124	129	134	132	129
S. New England	133.7	140	135	138	129	128	132
Mexican Highlands	134.2	125	110	139	142	148	141
Missouri Plat.-Glaciated	135.7	137	139	134	146	137	121
Aspen - Parklands	136.0	155	152	144	127	122	116
Missouri Plat.-Unglac.	141.8	148	146	143	144	135	135
S. Humid Coastal Belt	142.2	161	154	141	139	131	127
Allegheny Plateau	143.3	147	146	148	142	144	133
Central Rocky Mountains	145.3	195	143	138	128	136	132
Closed Boreal Forest	146.5	185	165	147	133	130	119
West Gulf Coastal Plain	148.2	151	142	160	153	144	139
Ridge and Valley	149.0	150	151	148	155	146	144
W. Lake Section	150.7	158	152	150	143	154	147
Cascade Mountains	151.3	172	162	159	141	139	135
E. Lake Section	155.8	158	159	160	157	154	147
Upper Coastal Plain	169.8	173	173	179	163	163	168
Spruce-Hardwood Forest	194.2	196	162	209	200	201	197
Continental Average	115.5	126.9	114.9	114.2	111.3	109.3	117.9

Our examination of latitudinal gradients was rather brief in this paper, but our results are very similar to others reported in the literature. Latitudinal gradients have been recognized for nearly a century but only recently have they been examined in detail (Simpson 1964; Pianka 1966). Cook (1969) analyzed variations in breeding bird densities by overlaying a grid on range maps of breeding species similar to the method described by Simpson (1964) for mammals. Cook found an increase in the number of breeding species through the prairie region of the United States to about the Canadian border. Data from our survey routes (fig. 4) show a similar trend in numbers of species. Cook hypothesized that historical factors, such as repeated glaciations, influenced the present pattern. We believe the latitudinal gradient in our species data through the central United States and Canada is influenced (at least proximally) by a more heterogeneous landscape in the North that attracts and holds more species than farther south. Even though there were fewer species recorded in the South, the distribution of individuals among the species was similar to northern areas; thus similar species diversity indices were exhibited.

Cook (1969) recorded bird species density decreased toward the end of a peninsula. Our data are similar to his from the Appalachian Mountains to the tip of Florida, with a gradual decrease through 8 strata in the average number of species recorded (58, 55, 53, 51, 52, 51, 49, 40, respectively).

Tramer (1974) found the number of forest-dwelling species to increase from east to west in North America and from north to south in western North America, but declined from the Great Lakes southward in eastern North America. Our data are somewhat contrary, since a southwest to northeast trend is more apparent, but we did not census strictly homogeneous habitats nor did we restrict our survey to only forest-dwelling species. A latitudinal trend in the West appears rather difficult to delineate because of the radically different mixture of physiographic regions. In the East, our data generally agree with Cook's but primarily from the mid-Appalachians southward.

Our data indicates that closely related habitats, or habitats of similar physical profiles and complexities, exhibit similar species diversities. A continuum in breeding bird communities exists between the xeric areas of the West and Southwest to the mesic forest complex of the Northeast. Those physiographic regions dominated by desert type vegetation have relatively simple avifauna containing a few prominent species, while the ecological strata containing complex evergreen or hardwood mixtures have a relatively large species composition evenly distributed over the entire avifauna.

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Avian Behavior and Habitat Management¹

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Abstract.--Implications of avian behavior in habitat management are assessed via literature survey. Territoriality, dispersion, and habitat selection are particularly germane to management policies. Consideration of each results in applicable management recommendations and targeted research needs, which are enumerated in the summary.

INTRODUCTION

Human alteration of natural habitats inevitably brings changes in species composition and population densities. The extent to which these changes will adversely affect human and wildlife populations in the long run has received increased attention in recent years. Evidence for this is seen in the compilation of lists of rare and endangered species, in tighter restrictions on collecting and transporting plants and animals, and in the gathering of specialists for symposia such as this one. Implicit in the theme of this symposium is cognizance of the fact that habitat management to enhance one aspect of land use adversely affects other aspects. Habitat management, therefore, must be seen as a strategy of compromise in which gains and losses are weighed against a land use ethic in the sense of Aldo Leopold. Thus our charge here is not necessarily to identify means for managing lands solely to enhance their suitability for certain species of nongame birds, or even for nongame species in general. Rather we must develop a framework of general concepts which, when incorporated into a total land management program, will minimize detrimental effects on nongame bird populations resulting from the spread of Earth's cancerous growth of human beings.

Thorough understanding of the role of behavior in processes of avian habitat utilization, habitat selection, and dispersion

patterns is an important part of formulating management programs compatible with maintenance of bird populations. At a recent international colloquium on bird protection in Antwerp, Belgium, three papers (Mörzer Bruyns 1972, Murton 1972, and Buwet 1972) treated different phases of behavior. These and other topics are discussed in the present paper, which is not an exhaustive survey but rather just the top of an iceberg of literature and ideas. Four major subjects--mating systems, dispersion, territoriality, and habitat selection--are summarized here. In each case current thinking relative to basic principles is reviewed, as it is almost axiomatic that effective application of principles depends first on understanding them. Selected examples are provided when appropriate and/or available. Finally, management implications are discussed in the form of recommendations at the end of each section. All recommendations are brought together in the summary. Space limitations preclude inclusion of all relevant literature. Instead key studies are used to illustrate concepts, and major review articles are cited to provide quick access to other literature on each topic. Scientific names of all bird species mentioned in the text are listed in the appendix.

MATING SYSTEMS

Concept Development

Orians (1969) and Wiley (1974) summarize factors important in evolution of avian mating systems. Critical to this phenomenon are the following facts and/or widely accepted views: (1) Prolonged parental care of eggs and offspring is the rule among birds. (2) Male birds, unlike male mammals, are morphologically

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as well-equipped as females to care for their young. (3) Mate selection in birds usually is the province of females. (4) The result of the above is that most bird species are monogamous because natural selection has favored females which chose unmated males as mates, thus increasing the likelihood of male help in rearing young. In fact about 90-95% of all bird species are monogamous (Verner and Willson 1966, 1969; Lack 1968). Most of the remaining species are polygynous or promiscuous; although a few species exhibit varying patterns of polyandry (see Jenni 1974, for recent review).

Avian polygyny and polyandry were for years excused as by-products of skewed sex ratios among adults in breeding condition. That view was first challenged by Orians (1961) as he sought to explain the adaptive significance of polygyny in Red-winged and Tricolored Blackbirds. Efforts to establish the sex ratio of adults in breeding condition were admittedly beyond the scope of Orians' investigations, although he cited papers indicating that adult sex ratios of some polygynous passerine birds probably do not differ so much from 50:50 as suggested by sex ratios of breeding adults. Furthermore, Orians showed that experimental removal of territorial male redwings resulted in their quick replacement by other adult males in breeding condition.

Verner (1963, 1964) discovered that sex ratios among adult Long-billed Marsh Wrens during the breeding season did not differ significantly from unity. In several instances females were known to select as mates males which already were paired, in spite of the fact that bachelor males were defending territories nearby. These facts forced the conclusion that polygyny must, in certain conditions, be selectively advantageous to females as well as to males. If available males and/or their territories differed sufficiently with regard to some requisite for successful breeding, females might rear more offspring alone when mated to a superior male or nesting on a superior territory than they could mated to an inferior male or nesting on an inferior territory. If female birds actively discriminate among males and/or their territories, then the basis for such discrimination provides information useful in habitat management for the species in question.

Examples

Pairing success of male Long-billed Marsh Wrens in various populations in Washington state increased with increasing territory size, with increasing area of emergent vegetation

within territories, and with increased numbers of courting nests built by males. This may mean that females discriminated among available territories on the basis of food availability, eventually nesting in that territory in which they spent the least amount of time getting a full belly (Verner 1963, 1964; Verner and Engelsens 1970). The result was that some males held territories all season as bachelors, while about an equal number of other males obtained two mates. Secondary females (those acquired second by bigamists) received less assistance from their mates in rearing broods. In some cases they received no assistance at all.

Verner and Engelsens (1970) found a significant negative correlation between pairing success and the percent of bulrush (*Scirpus acutus*) in territories of male Long-billed Marsh Wrens in eastern Washington. Monogamists and bigamists exhibited a significant tendency to place nests in cattail (*Typha latifolia*) rather than bulrush. Bachelors, however, did not. Moreover, bachelors failed to complete a significantly higher percentage of nests placed in bulrush than in cattail. This was not true of monogamists or bigamists. Nests in bulrush slipped down the smooth stems and/or were blown loose more often than nests in cattails. This probably accounts for the preference for cattails as nesting cover. It also suggests that a high percentage of bachelors were yearlings that had to learn not to build nests in bulrush.

Subsequent studies of polygynous bird species have addressed the same question and revealed varying sorts of environmental cues apparently important to females in selecting a nesting area. Willson (1966) showed that pairing and nesting success of male Yellow-headed Blackbirds correlated with the total length of vegetation/open water interface in their territories. Site selection could be related to safe nesting places (nests were always located on lakeward edges of vegetation) and/or to food availability. Recently emerged damselfly (Odonata) larvae comprised the principal food source for nestlings, so the length of vegetation/open water interface could influence the total number of prey items near nests. Willson reported that yellowhead territories were small where emergent vegetation was patchy and large where vegetation occurred in larger, denser stands. Fewer plant stems per unit area would tend to concentrate emerging odonate naiads, making such areas more efficiently exploited.

Selectivity in mating preference by female Red-winged Blackbirds was reported by Linsdale (1938) to be influenced by cattail density within territories of males. Intermediate

cattail densities were preferred over very sparse or very dense stands. This was also documented by Holm (1973), who found no correlation between harem size and territory size or between harem size and the amount of food taken by females from the territory. Females selected nesting sites in territories containing mostly cattails as opposed to bulrush, and more females bred in areas of scattered than dense cattail growth.

Zimmerman (1966) and Harmeson (1974) found pairing success among Dickcissel males depended on availability of nesting cover in their territories. Territories of bachelors were significantly smaller than those of monogamists and bigamists and contained a higher proportion of grasses, a lower proportion of forbs, and substantially less of the tall vegetation preferred by females for nest cover.

Martin (1971) found Bobolinks to be similar to Dickcissels. Territories of bachelors, monogamists, bigamists, and trigamists all exhibited significant differences in density of large forbs (the only suitable nest cover when nesting was initiated). According to Martin, territories of the different classes of males also differed significantly in "percent coverage of grasses, sedges and forbs, shading properties of the vegetation, and the vegetative height profile." Bachelors held territories most deficient in features important in female nest site selection, monogamists and bigamists held territories intermediate in quality, and trigamists held the best territories.

Limited availability of suitable nesting sites also may account for evolution of polygyny in many species of tree-nesting, savannah species (e.g. African weaverbirds, Crook 1964; Australian Magpie, Carrick 1963). The same may be true of several species which nest in cavities but do not excavate their own nesting sites (e.g. Pied Flycatcher, Haartman 1956; Collared Flycatcher, Löhrl 1949, 1959; House Wren, Kendeigh 1941; European Wren, Armstrong 1955). Curio (1959) found bigamous and bachelor males in a population of Pied Flycatchers and observed that bachelors generally had less suitable nest cavities. Haartman (1969) reviews the relationship between nest sites and mating systems.

Comparative investigations of avian mating systems have revealed another aspect of their relationship to habitat. Verner and Willson (1966) showed that nearly all North American passerine species in which polygyny is exhibited by at least 5% of the males are

characteristically found breeding in two-dimensional habitats (i.e. prairies and marshes). Marshes, especially, must provide conditions favoring evolution of polygyny, as at least half of the marsh-nesting passerine species of North America regularly exhibit polygyny. Less than 1% of the forest-breeding species do so. The situation is similar among weaverbirds, among which most forest species are monogamous and most savannah species are polygynous (Crook 1964).

Marshes and savannahs provide situations where available nesting cover is restricted relative to available foraging areas, so a male may be able to defend a disproportionate share of ideal nesting cover and thus attract a disproportionate share of females (see Orians 1961, 1969).

Verner and Willson (1966) point out that all productivity in two-dimensional systems is concentrated within a narrow vertical zone easily open to exploitation by a single bird. The result is a greater potential for concentration of food resources in marshes than in forests. Consequently, extremes in the range of differences in food density between territories occupied by males are potentially greater in marshes than in forests. Selection for polygyny, according to the argument presented here, depends on such differences between occupied territories, whether they be in terms of the suitability of nesting cover or in terms of the density of food supply. The latter seems the most likely factor involved in evolution of polygyny in Long-billed Marsh Wrens, and it also may be a determinant of the mating system in Yellow-headed Blackbirds.

Management Implications

Polygyny provides field ornithologists a means for ranking various territories in order of their suitability, assuming that increased pairing success of territorial males is indicative of their occupying more suitable sites. Recent investigations of these systems indicate that food supply may be a primary factor in habitat selection for a few species. Availability of superior nesting sites apparently is more often a critical factor in the selection of breeding sites by females of polygynous species. Synthesis of data available on polygynous species in two major habitat types suggests possible management practices to maximize their suitability for species concerned: (1) Marsh habitats of intermediate stand density, with substantial vegetation/water interface, are more suitable than very sparse or very dense, uninterrupted stands. Cattails are preferred over bulrush. Cattle

frequently open up dense stands of cattail, so appropriate grazing practices might be employed as one means of improving marsh habitats for nongame birds. (2) Prairie habitat providing a heterogeneous mosaic of grasses and forbs is more suitable than uniform stands of either. Controlled burning programs have been used with success in reclaiming native prairie vegetation from disturbed sites and in creating greater variety among the plant species (e.g. see Smith and Owensby 1973, Anderson 1973).

The procedure of using male pairing success as an indicator of habitat suitability might be modified to evaluate habitats of monogamous bird species. It is reasonable to presume that males occupying the most suitable territories should be paired first, and that successively later pairing should reflect decreasingly suitable habitat. Verner (1964) used both techniques (i.e. male pairing success and order in which males were paired) to assess habitats of Long-billed Marsh Wrens and reached identical conclusions with each method.

DISPERSION

Concept Development

Dispersion refers to the particular pattern of distribution of organisms within their habitat at any instant in time. It should not be confused with dispersal, which refers to the process of transport or movement by which organisms become distributed. Birds exhibit a wide range of dispersion patterns at all times of the year. Depending on species and season, birds breed, forage, and roost in various concentrations from lone individuals or pairs, to small, loosely aggregated flocks, to large and tightly concentrated flocks or colonies. Reasons for the evolution of these diverse strategies in various bird species have been the subject of a number of recent population studies and review articles (Brown 1964, 1969; Crook 1964, 1965; Horn 1968; Lack 1968; Brown and Orians 1970; Schoener 1971; Ward and Zahavi 1973).

Different dispersion patterns have been interpreted as adaptations evolved to optimize individual survival and reproduction in relation to resource distribution and/or predator defense. It is obvious that colonies of island-nesting seabirds represent an evolutionary adjustment to limited breeding sites within economical foraging distance of ample food supplies. That predator avoidance is also a factor in the choice of breeding colonies by such species is suggested by island nesting of some of the same species, or of closely related species, in lakes or rivers. For example, White Pelicans

are island nesters at Yellowstone Lake (Schaller 1964), while Caspian Terns and Ring-billed Gulls nest on islands in the Columbia River and in Moses Lake in central Washington (Verner, personal observation). These birds restrict their nesting to islands while apparently comparable substrate is plentifully available onshore.

Brown (1964) asserted that "when a food supply cannot be feasibly defended, because of its mobility or transient nature, generally no territorial system is evolved to defend it; and the territory, if present, may be restricted only to the nest and the area reachable by the parents on the nest. Such cases are found in colonial sea birds, nomadic and social feeding passerine species, and aerial feeders. In these species the goal of increased or guaranteed food supply is unlikely to be attained through aggression." Crook (1964, 1965) and Lack (1968) pointed out that natural selection should favor colonial nesting only in places providing maximum security from predators, because colonies cannot be effectively concealed. These factors taken together reasonably explain nesting dispersion of species such as the swallows, swifts, some kites, the Tricolored Blackbird, and Brewer's Blackbird. Red-winged and Yellow-headed Blackbirds are intermediate between species which obtain all their food from relatively large territories and species which obtain all their food off their relatively small territories. Crook (1964) showed that nearly all forest-nesting weaverbirds of Africa, in habitats where resources are relatively evenly distributed, defend solitary territories and obtain their food, cover, and nesting sites from them. All African, seed-eating weaverbirds of open country nest in neighborhoods or colonies and forage together in common feeding grounds. Their food is abundant only for short periods following the rainy season. Most of these species nest in dense colonies high in the foliage of scattered trees on the savannah. Crook emphasizes the protection afforded from predators by the sites and forms of nest construction of these weavers. Both Crook (1964) and Lack (1968) refer to species whose breeding dispersions vary with variations in their habitats.

Examples

Horn's (1968) analysis of the adaptive significance of nesting dispersion in Brewer's Blackbirds is exemplary. These birds fed their young primarily on the naiads and teneral of damselflies (Odonata), distribution of which was unpredictable in time and space because of diurnal variation in peaks of emergence and the effects of wind in concentrating the insects at leeward edges of lakes. Colonial nesting

apparently permitted members of the colony to locate new food sources by following successful individuals. This system should develop only when the food source first located by one individual is more than that individual alone can consume (Ward 1965; Horn 1968; Ward and Zahavi 1973; and especially Krebs 1974).

Horn also showed that the density of nests within colonies varied with colony shape, nests being farther apart in linear (i.e. elongated) colonies than in open (i.e. tending more toward circular) colonies. The birds defended against potential predators to a radius at least four times the mean distance between nests. In open colonies, closer spacing of nests put each within the radius of defense of more pairs, but it also resulted in less searching for nests by a predator once a colony was located. In linear colonies, a given nest could be included within many defense radii only if the nests were unusually close together in a row. Such concentration would probably make the discovery of all nests by a successful predator a very simple matter. Mean distance between nests was thus seen by Horn as a compromise between selection to bring nests closer together to take advantage of overlapping defense radii and selection to spread them out to minimize a predator's success in locating nests.

Post (1974) reported alternate strategies of breeding dispersion among Seaside Sparrows in response to differing environmental conditions. Large, all-purpose territories occurred in altered habitats, and smaller grouped territories from which birds foraged at distant sites were formed in unaltered salt marsh habitat. Nest site availability and susceptibility to predation were the principal factors judged by Post to influence which dispersion pattern was exploited by these birds.

Another excellent example of this phenomenon was provided by the study of Carothers, et al. (1974) on breeding dispersion of riparian birds in Arizona. They studied bird populations in two contrasting, riparian habitats: (1) mixed deciduous forests with much undergrowth, and (2) essentially single-species stands of cottonwood with little or no undergrowth. They found marked contrasts in avian abundance and diversity, territorial relationships, foraging behavior, and mean body size between species in the two habitats. A significantly higher percent of bird species (57%) in the mixed forests maintained large territories in which they did all their feeding. Only 22% of the species in cottonwood stands gathered all their food from the territory, most species foraging extensively over the river and/or adjacent agricultural lands.

Territories averaged smaller in the cottonwoods, and densities of breeding pairs were much higher there in every case. Carothers, et al. (1974) singled out Starlings, Western Kingbirds, and Cassin's Kingbirds as examples of species whose dispersion pattern and territorial behavior changed in response to habitat differences. This flexibility enabled these species to exploit relatively rich food sources in areas lacking safe nesting sites, because safe nesting sites were available nearby. Thus, within a single species differential dispersion patterns and habitat exploitation strategies were shaped by an interaction between selection of safe nesting sites and utilization of food sources variously predictable in space and time.

Even during non-breeding periods food distribution, safe roosting sites and advantages of flocking in predator defense are apparently of primary importance in determining avian dispersion patterns (Cody 1974). The role of food distribution was shown experimentally by Zahavi (1971) to determine whether White Wagtails wintering in Israel form territories or feed in groups. Zahavi's field observations of Great Tits in Israel indicate that defense or non-defense of winter territories was a function of food distribution in that species also.

Management Implications

Flexibility in dispersion patterns, as exhibited by some species, can be translated into applied practice in habitat management. Extensive agricultural lands, especially those near lakes or rivers, should have narrow belts of tree and shrub plantings to provide nesting cover for insectivorous birds. Many such species nest in substantially higher densities in these conditions, and their combined foraging on insects over the fields might be of economic importance as well. Current use of pesticides may negatively affect birds nesting in belt plantings, but that is another problem.

In the same vein, most highways and freeways in this country today have neatly mowed shoulders and center strips that are costly to maintain and preclude their use as nesting cover by birds. Especially in urban and suburban settings these strips have been planted with shrubs for beautification and to provide a traffic safety cushion. Many birds exploit these strips for nesting cover and foraging. Such plantings should be extended all along our highways with species of grasses, forbs, and shrubs appropriate to the combined goals of beautification, reduced maintenance cost, traffic safety, and nesting cover for birds adjacent to agricultural lands.

TERRITORIALITY

Concept Development

Historical development of the concept of territoriality in bird life can be explored in a series of landmark papers by Howard (1920), Nice (1941), Lack (1954, 1968), Hinde (1956), Wynne-Edwards (1962), Brown (1964, 1969), and Stokes (1974). Territoriality involves exclusive priority over space. Authors differ in their definitions of territory, from the classic one involving defense (Noble 1939, Hinde 1956, Emlen 1957, Brown 1969), to Pitelka's (1959) view that "territory should be defined as an exclusive area, not merely a 'defended' one", to Willis' (1967) modification involving spatial variations in dominance status among birds otherwise apparently spaced out on exclusive territories. Ecologically, our interest lies in the fact that territoriality results somehow in the spacing of birds over available habitat and thus in exclusive resource utilization. I am in full agreement with Pitelka (1959) and Schoener (1968) on this point.

Factors related to colonial nesting were discussed in the previous section, so analysis here is restricted to species which nest solitarily. According to Lack (1968) nearly 90% of all bird species fall into this category, and the majority of those obtain most or all their needs from the territory (Type A territory of Nice 1941), at least in temperate zones (see Karr 1971).

The great debate in avian territoriality focuses on a problem of singular importance to the theme of this symposium. Howard (1920) suggested that one function of territories is to space populations out over available resources, thus reducing population density. Others since Howard (especially Kalela 1954 and Wynne-Edwards 1962) have developed this notion in great detail, relying on group (i.e. inter-deme) selection as a mechanism for evolution of territorial behavior. Debate centers on this facet of the problem, as most students of avian behavior discount group selection as a viable mechanism of evolution. Space limitations preclude a lengthy discussion of the issue here. Those interested in pursuing the topic should see especially Lack (1954, 1968), Wynne-Edwards (1962), Brown (1964, 1969), Wiens (1966), and Williams (1966). Suffice it to say that I believe group selection has had nothing to do with evolution of territorial behavior in birds, but I do not believe that need be an issue here. What concerns us is whether or not territory defense ever limits the number of breeding birds in an area.

Evolution of territoriality is fully consistent with classical Darwinian selection, and one of its effects (not causes) may be the limitation of the density of breeding birds. Perhaps the most significant statement ever published on this point is that of Brown (1964): "The aggressiveness necessary to establish a large, exclusive territory may gain relatively little in terms of food, cover, and mates when they are already in adequate supply for the population as a whole, but by mere possession of an opportunity to breed, the territory owners would leave more reproducing offspring than the nonowners. As long as counter selection against aggressiveness were weak, aggressiveness per se would be maintained in the population merely by the exclusion of less aggressive birds from breeding." Unfortunately the significance of this statement seems to have been overlooked by practically everybody, with the exception of Chitty (1967). Note that it follows from Brown's statement that natural selection could, if conditions were right, lead to evolution of territories much larger than needed to ensure the requisites of survival and reproduction, if such large territories prevented breeding by some members of the population. The net effect would be limitation of breeding density.

Brown (1969) disputes the view that limitation of breeding density has been established as a common effect of avian territoriality. His is an excellent, exhaustive, and exacting analysis of published cases ostensibly showing territorial limitation of breeding density. Brown argues that three conditions must be met before field data confirm that territoriality limits breeding density: (1) It must be proven that individuals physiologically capable of breeding are not doing so. (2) It must be shown that their failure to breed is a direct result of the territorial behavior of other birds in the population. (3) Females must be among those in the excluded group. Brown urges caution in extending results from a single population to an entire species, or to another species, but concludes that some populations show evidence of limitation by territorial behavior. I believe we will find that territoriality often limits breeding density in a wide variety of bird species. Brown's (1964, 1969) clear statement of the sorts of evidence required to prove such cases will likely influence data gathering by field workers to assure that they satisfy all conditions. Examples are the recent studies of Watson and Jenkins (1968), Holmes (1970), Harris (1970), Krebs (1971), Ridpath (1972), and Manuwal (1974) on the Red Grouse, Dunlin, Oystercatcher, Great Tit, Tasmanian Native Hen, and Cassin's Auklet, respectively. Each case seems to establish

the role of territoriality in limiting density of a breeding population. A recent review is provided by Watson and Moss (1970).

Territory Size

Effective management of any territorial species necessarily involves consideration of territory size and its relationship to total land required to provide enough territories so a population can maintain itself indefinitely in an area.

Territory size varies enormously from species to species (see tabulation below) and even within species. For example, Tompa

Approximate mean territory sizes of selected North American Birds (Welty 1962).

Species	Area in m ²
Least Flycatcher	700
American Robin	1,200
Red-winged Blackbird	3,000
House Wren	4,000
American Redstart	4,000
Song Sparrow	4,000
Ovenbird	10,000
Black-capped Chickadee	53,000
Western Meadowlark	90,000
Great Horned Owl	500,000
Red-tailed Hawk	1,300,000
Bald Eagle	2,500,000
Golden Eagle	93,000,000

(1964) found that Song Sparrow territories on Mandarte Island, British Columbia, averaged about 1/10 the size of those studied by Nice (1943) in Ohio. Territory sizes of Long-billed Marsh Wrens in eastern Washington ranged from 83 to 1670 m² and exhibited increasing means from bachelors (517 m²) to monogamists (642 m²) to bigamists (685 m²) (Verner and Engelsen 1970). In western Washington Long-billed Marsh Wrens defended territories averaging 1189 m², 1826 m², and 3236 m² for bachelors, monogamists, and bigamists, respectively. At a nearby marsh during the same time period the comparable sizes were 909 m², 1321 m², and 1616 m² (Verner 1964). These variations probably resulted from a number of factors, among them the nature of the marsh and ages of the defending males. Marshes providing large expanses of emergent vegetation generally supported larger territories than marshes confined to narrow strips along margins of lakes or streams. It is not certain that age was a factor in

territory sizes of these wrens, but territory size increased with increased pairing success of the males. Age has been related to pairing success in several polygynous species (e.g. Red-winged Blackbirds, Orians 1961; Yellow-headed Blackbirds, Willson 1966; House Wren, Kendeigh 1941). Moreover, territory size was shown to increase with age in a few species (e.g. Great Tit, Dhont and Hublé 1968; Tasmanian Native Hen, Ridpath 1972).

Schoener (1968) analyzed factors involved in intraspecific and interspecific variation in territory size. In addition to factors mentioned above, Schoener found evidence of intraspecific variation in territory size as a function of: (1) stage of the breeding cycle, territory size decreasing in some species with progression of the nesting cycle; (2) habitat quality, territories being larger in habitat judged by researchers to be marginal for the species (but see Catchpole 1974); (3) population density, territories being smaller when more individuals seek territories at the beginning of the breeding season; and (4) numbers of individuals of other species breeding in the area, though no sound evidence is brought forth on this variable. Schoener's major contribution was his analysis of factors affecting interspecific variation in territory size.

Considerations of body size and diet permitted Schoener to explain most of the statistical variance in territory size among species. Species were grouped into categories of animal, omnivorous, or herbivorous diet as follows:

- A - 90-100% animal food
- AO - 70- 90% animal food
- O - 30- 70% animal food
- HO - 10- 30% animal food
- H - 0- 10% animal food

Among predatory specialists (category A) 91.5% of the variance in territory size was accounted for by species differences in body weight. Among herbivorous specialists (H) 78.6% of the variance was explained by differences in body weight, but Schoener's sample consisted of only three species. Correlations for other feeding categories were not significant (see fig. 1). Schoener observed "that the greatest territory sizes for a given weight appear to be for birds which have the greatest proportion of animal matter in their diets. Certain omnivores and herbivores have the smallest territories for their biomass. These results are in accordance with the probable relative food densities for the different categories. Herbivores and omnivores would be expected to feed on denser food than insect or vertebrate predators. The omnivores with the largest

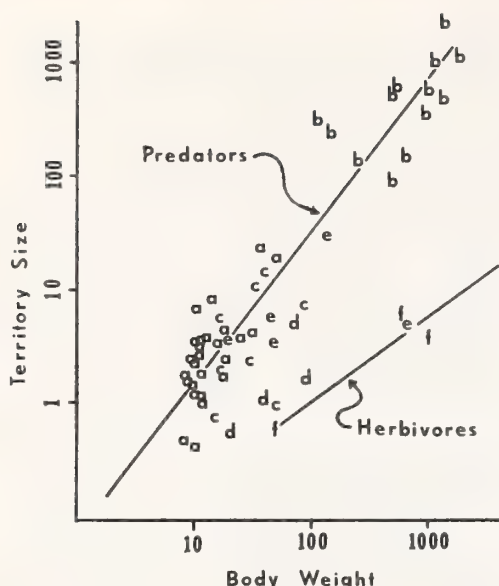


Figure 1.--Relationships between territory size (acres) and body weight (grams) for birds of different feeding categories. Symbols designate varying percentages of animal food as follows: a = 90-100% (mainly arthropods), b = 90-100% (mainly vertebrates), c = 70-90%, d = 30-70%, e = 10-30%, and f = 0-10%. Adapted from Schoener (1968).

territories for their body weights are usually those consuming the greatest proportion of animal matter (AO)." Other important conclusions reached by Schoener were (1) that home ranges of raptors in two areas were significantly correlated with prey density, (2) clutch size did not correlate with territory size in any group tested, (3) probably no correlation existed between territory size and number of birds defending the territory or feeding young, and (4) the habit of obtaining most or all food from the territory varied according to diet, being highest among predatory specialists (91.7% of species in category A, 50.0% in category AO, 16.7% in O, 33.3% in HO, and 42.9% in H).

Body Size, Territory Size, and Local Extinction

Careful studies of the reasons for local extinction of bird populations are practically non-existent. One exception is the recent report of Willis (1974) on declining numbers of bird species on Barro Colorado Island since its establishment in the Panama Canal Zone in 1910-14. The island, in Gatun Lake, is separated from the nearest mainland by about 500 m of open water. Between 1914 and 1923, when the island was established as a biological reserve, patches of forest were cut down.

"Much of the eastern half of the island is medium-height forest, probably under 100 yr old; much of the western half is tall forest, probably mature but almost certainly not virgin..." (Willis 1974). In addition to comparing present composition of breeding bird species on the island with earlier censuses, Willis undertook a careful, 10-year study of the population dynamics of three species of ant-following birds. Birds were individually color-banded and data were gathered on mortality, natality, movements, and population changes.

Early census work indicated that 209 bird species nested on Barro Colorado when it was established as a reserve in 1923. Forty-five species (22%) have disappeared without replacement and a number of other species appear likely to disappear from the island in the near future. Most species (71%) which became locally extinct were birds characteristic of second growth forest and probably would return to the island if new forest clearings were made. Thirteen species were inhabitants of woodland and forest, and eight of those nested or foraged near the ground where they may have been subjected to unusually heavy predation from mammals.

Among the seven species of ant-following birds (those which follow army ants to get most of their food from insects disturbed by the ants) known to be present on Barro Colorado in 1923, the largest in size had evidently disappeared by 1935. The second largest disappeared during the period of Willis' study; and the third largest declined to near extinction during the study period. Another species, the fifth largest among seven, declined to about half its original density during the study period. Territory size in these species decreased with body size. The two extinct forms did not, in Willis' experience, cross open areas such as Gatun Lake, so local extinction may mean no replacement. J. Diamond (in Willis 1974) "found most forest birds, even strongly flying ones, absent on a forested island only 55 m off the coast of New Guinea." This may be typical for many species adapted to dense forest undergrowth and is certainly an important behavioral consideration in habitat management, especially in the tropics.

Willis was unable to ascertain definitely the causes for local declines and extinctions of birds in his study, but he documented unusually high mortality rates in the three bird species intensively investigated. Replacement rates were inadequate in two of the three species, and Willis argues that even if calculated mortality rates were atypically high because of temporary conditions on Barro Colorado, the island's small size likely contributed to local extinction because it does

not provide sufficiently large areas of suitable breeding habitat to accommodate many breeding pairs. Little variety in habitats reduces the chance of there being favorable refuges where breeding can succeed even when temporarily adverse conditions interfere with breeding success over most of the range. Isolation is critical in preventing repopulation from nearby areas where populations have been maintained. Willis observed that "perhaps it matters less why animals in tropical parks disappear than it does that animals do disappear for practically undetectable reasons. We then realize that conservation theorems of general validity are needed rather than, or in addition to, specific techniques..." One such theorem suggested by Willis is that "arithmetic loss of space leads to geometric decline in the value of the remaining space." If we reduce the size of a nature preserve by 50%, we may reduce by 75% or more its value as a preserve. Based on this study, Willis urged that management of habitats for preservation of natural biotas incorporate the concept of maintaining corridors of suitable habitat connecting preserves. Species "could then shift temporarily to the favorable end of a gradient if their usual reserve was subjected to temporarily unfavorable conditions." I believe this recommendation is all the more significant because it was generated from a study of birds, organisms whose powers of dispersal are unexcelled.

Interspecific Territoriality

Many observations and recommendations made above in relation to intraspecific territoriality extend to those species pairs or groups which maintain interspecific territories. Orians and Willson (1964) reviewed known cases of interspecific territoriality among birds. Examples of such species pairs from North America, as cited by Orians and Willson, include Red-winged and Yellow-headed Blackbirds, Red-winged and Tricolored Blackbirds, Red-winged Blackbird and Common Grackle, Eastern and Western Meadowlarks, Golden and Black-bellied Plovers, Red-tailed and Red-shouldered Hawks, Great Horned and Barred Owls, White-throated and Song Sparrows, Red-bellied and Golden-fronted Woodpeckers, Anna's and Allen's Hummingbirds, Rufous and Calliope Hummingbirds, and Plain and Bridled Titmice. This is not an exhaustive list but provides an idea of the sorts of species and habitats involved in interspecific territoriality. Cody (1969, 1973, 1974) concluded that general conditions favoring evolution of such behavior reduce to three circumstances: (1) simple habitats providing a narrow range of resource types, (2) species which are food specialists, and (3) many

other species present to limit the extent of species packing. Murray (1971) suggested an alternative explanation for interspecific territoriality among birds. The important point is that interspecific territoriality occurs and could contribute to reduced population density of species involved.

Management Implications

There is little doubt that avian territoriality limits population density in some circumstances. It is equally likely that more than one breeding pair of any species is essential to the maintenance of that species. The difficulty is that avian ecologists cannot tell us for any species the minimum number of breeding pairs required to maintain the population or the smallest area of suitable habitat essential to accommodate indefinitely that number of pairs. These are important areas of research needed to provide information vital today in land management, yet it is unrealistic to assume that even a most ambitious research effort would soon yield the data we need on a substantial number of nongame bird species of North America.

A better operational approach might be to concentrate effort on identification of key species, populations of which can serve as indicators of the vitality of avian populations in general. What we know of territory size and its effects on population density, and about ecosystem organization, especially trophic structure, suggests that we should begin looking for indicator species among larger carnivores (hawks, owls, larger insectivores). First, these species have larger territories. Their maintenance should ensure that at least most of the smaller species in a given ecosystem would be able to maintain their populations. Second, they depend on lower trophic levels for their food supply--if they find food enough to persist, populations at lower trophic levels must be in pretty good shape also. Finally, biological concentration of toxic environmental contaminants results in maximum concentrations in top carnivores. Ill effects among these species probably forewarn of similar effects at lower levels unless steps are taken to curtail application of such substances to the environment.

Willis' recommendation that corridors of suitable habitat be maintained to connect preserves otherwise isolated by habitats unsuitable to species using the preserves needs serious consideration. It probably is more applicable for tropical species, which are more sedentary than temperate zone species. It also is relevant only for those species which are non-migratory and which will not cross long

stretches of unsuitable habitat. While these conditions probably are not often applicable to birds in temperate regions, nonetheless mobility between patches of suitable habitat undoubtedly decreases with increasing distance between them. Interconnecting corridors may not be so critical in temperate zones, but the dispersion pattern of preserves no doubt can be such as to optimize mobility of birds from one preserve to another. Local extinction would thus be only short-term. Research is needed on this topic.

HABITAT SELECTION

Concept Development

Evolutionary Considerations

Over the long span of evolutionary time all species have become adapted to survive and reproduce effectively in a limited range of habitat conditions. Obviously some species can make a go of it in a wider variety of habitats than others, but no species is equally fit in all environments. The mobility of birds, particularly migratory species, often results in their being exposed to a variety of habitats between the times of hatching and breeding. Consequently they should have evolved to make appropriate responses to different habitats, not settling in unsuitable ones but instead settling to breed only in those sites providing all essential requisites for maximum reproductive success. This point is argued to its extreme by Hildén (1965): "The selection mechanism guides the birds to an environment meeting their ecological requirements.... Where several territories releasing the settling reaction are available, the bird chooses the best of them...." While Hildén fails to present conclusive proof that birds are capable of differentiating the best territory among those available, I agree that this tendency should be favored by natural selection and that we should be able to produce evidence of it. We cannot, however, view the world as a bird does, nor can we control natural environments to permit critical experimentation on this question. Still we have much evidence about which environmental features are important to various bird species in their selection of habitats--e.g. Lack (1933), Lack and Venables (1939), Kendeigh (1945), Klopfer and Hailman (1965), Gannon (1966), but especially Hildén (1965--all subsequent references to Hildén are based on his 1965 paper).

Proximate and Ultimate Factors

Hildén emphasized the distinction between proximate factors and ultimate factors

in habitat selection by birds. Proximate factors are those features of the environment which provide the direct stimuli leading either to a positive or a negative response to a given environment. For example, suitable nest cavities are important in selection of breeding territories by Pied Flycatchers and Great Tits (Haartman 1954, 1956). Ultimate factors involve those features of the organism's environment which make a particular response evolutionarily advantageous. As Hildén correctly stated, certain features of the environment may be both proximate and ultimate factors. In many instances, however, proximate factors are not directly of consequence in the adaptiveness of a given response but nonetheless result in a response which is adaptive for other reasons. For example, the Lapwing selects its breeding territory some time before conditions are suitable for breeding. Klopfer (1954) believes an important proximate factor releasing habitat selection is meadow color, gray-brown being chosen and green avoided. Grass on gray-brown sites does not grow so tall as on green sites, and Lapwings are better adapted to low grass habitats. Meadow color (a proximate factor) has only an indirect evolutionary consequence, since it is an effective predictor of later grass height (an ultimate factor).

Another example which serves well to clarify the distinction between proximate and ultimate factors is the seasonal change in pelt color of Snowshoe Hares (Lepus americanus). These mammals, at least in parts of their range, acquire a white coat in winter and a dark coat in summer. The adaptive significance of coat color clearly relates to the appropriate cryptic advantages on snow-covered or bare ground. But it is not the first appearance of snow which triggers pelt color change. The change begins some weeks prior to the mean date of the first persistent snow. Possible proximate factors serving to stimulate pelt color change include decreasing photoperiod, declining mean temperatures, and autumn leaf drop. None of these factors, per se, makes having a white pelt selectively advantageous, but each of them is correlated with an event in the near future which does.

Natural selection should favor evolution of organisms' responses to environmental stimuli (proximate factors) which most closely correlate with conditions vital to survival and reproduction (ultimate factors). If the ultimate factor is present (as in the case of nest cavities) at the time a response is made, then we should expect the ultimate factor to function as the stimulus (i.e. as the proximate factor). These concepts are dealt with in greater detail by Baker (1938), Svårdson (1949),

Lack (1954, 1966, 1968), and Orians (1962). Proper habitat management requires knowledge both of the proximate and ultimate factors involved in habitat selection. Ultimate factors are vital to successful reproduction, but suitable habitats will not be selected if proximate factors are absent.

Inter- and Intraspecific Competition

It is generally agreed among ecologists today that interspecific competition tends to reduce the range of variability in habitat utilization by a given species, while intra-specific competition tends to increase that range. Svårdson (1949) provided an early review of these concepts, with examples from birds, and a rigorous, recent review is found in Cody (1974). Interaction between intra- and interspecific competition should vary with the number of ecologically similar species occurring together in a habitat. Theory is borne out by fact in the case of birds when comparisons are made of the variety of habitats exploited by island and mainland populations of the same species. Island habitats typically support fewer bird species per unit area than do adjacent mainland habitats. It has now been shown for several bird species that island populations not only exploit a greater variety of habitats than their conspecifics on the mainland, but they also tend to utilize a greater variety of food sources within habitats (e.g. Svårdson 1949, Crowell 1962, Grant 1968, Diamond 1971, Terborgh and Faaborg 1973, Yeaton 1974, Yeaton and Cody 1974, and Cody 1974).

Bases for Habitat Selection

Identification of key environmental features in habitat selection by birds is extremely difficult, and only in rare instances have field studies established with little or no doubt what some of these factors are. Hildén's review covers the general range of features probably important in habitat selection. Some species select on the basis of one or a few primary factors, while for others no single factor is of primary importance. Examples of the kinds of features important in habitat selection follow.

Food

Hildén argued that food is not usually an important factor in habitat selection, because most bird species are not highly specialized in their diets. Roberts (1934) concluded that most species of Iceland birds eat whatever food can be obtained with least difficulty. Similarly, Hespenheide (1971) found little evidence of taxonomic specialization in food taken by flycatchers, swallows,

vireos, or terns. These groups appear to subdivide the environment more on the basis of spatial separation than food specialization. Haartman (1954) concluded that Pied Flycatchers and Great Tits exhibited a decided preference for forests dominated by deciduous trees, as opposed to conifers, and that this selection was little, if any, affected by differences in food availability in the contrasting habitats (but see Balen, 1973, for a factually-documented, contrary view). Hildén concluded that "the food factor seems not to have had any great significance in the evolution of species-specific habitat requirements; rather, the species have begun to use the food that is easily available in an environment selected on other grounds." Again, later, Hildén wrote: "In most species food does not seem to have any proximate effect on habitat selection." These statements may be true for a large number of bird species but I question the propriety of extending such a generalization to most bird species on the basis of a few studies indicating generalized feeding habits. Hildén acknowledged the importance of food in habitat selection of specialists such as crossbills and Arctic and boreal predators that exploit dense populations of rodents. He cited the importance of food in habitat selection by Golden Orioles (Durango 1955) and Greenfinches (Durango 1947). Numerous other cases of habitat selection believed based at least in part on adequate amounts of appropriate food are available in the literature. For example, nectar feeders of various families commonly select breeding and wintering habitats on the basis of the abundance of preferred flowers (see Stiles 1973; Wolf 1975). Orians (1961) speculated that Tricolored Blackbirds select a breeding marsh because of its proximity to a rich food supply. Female Long-billed Marsh Wrens may select breeding sites on the basis of how rapidly they can obtain food from territories of various males in the vicinity (Verner 1964, Verner and Engelsen 1970). Root (1967) concluded "that the abundance of such critical requisites as food and nest sites is directly involved in the habitat selection process" of the Blue-gray Gnatcatcher.

I believe food supply is probably a much more important factor in habitat selection than Hildén's review suggests. Admittedly food may be plentifully available in most habitats with other important factors serving to elicit habitat selection, especially for food generalists. But the absence of adequate food in otherwise suitable habitats clearly precludes effective utilization of those habitats, so natural selection would favor evolution of behavioral avoidance of such habitats. The fact is that for most species of birds we have little conclusive evidence on the matter.

Nest Sites

For many species the type of nest site utilized is a crucial factor in habitat selection. This is particularly true for those species of hole-nesting birds which do not excavate their own cavities (e.g. Kestrel, Elf Owl, Great Crested Flycatcher, Tree Swallow, Purple Martin, chickadees, Winter Wren, House Wren, Eastern, Western, and Mountain Bluebirds). Addition of man-made nests to unoccupied habitats has resulted in their selection for breeding by a number of species, such as the Pied Flycatcher and Great Tit (Haartman 1954, 1956), the House Wren (Kendeigh 1941), and bluebirds (Power 1966, Ligon 1969). In Finland the Goldcrest is restricted in its nesting to spruce forests, because only the drooping branches of these trees provide an adequate nest site (Hildén). The related Ruby-crowned Kinglet in North America is similarly specialized in its nesting behavior. In eastern Washington and northern Idaho I have found nests of this kinglet only in the drooping outer branches of Douglas Fir (Pseudotsuga menziesii). Numerous other species (e.g. Cliff Swallow, swifts, many colonial sea birds) have similarly restrictive nest site specializations which presumably affect their habitat selection, but care must be taken not to assume a species is inflexible in nest siting simply because we always find their nests in similar places.

Evidence for differential selection of cattails over bulrush as nesting cover by Long-billed Marsh Wrens was discussed above in reference to mating systems. If other conditions critical to breeding are suitable, however, these wrens will place their nests in what must be regarded as atypical cover. For instance, I once found a breeding population of Long-billed Marsh Wrens on the eastern outskirts of Kirkland, Washington, whose nests were placed in emergent shrubs (Spiraea douglasii). Another colony in which nests were supported by tall, dense grass in a flooded field was found just south of Kirkland. In both cases no cattails were available but there were safe nesting sites and food apparently was plentiful.

Catchpole (1974) described an interesting case in the Reed Warbler in Britain. This species has long been regarded as essentially restricted in its nest sites to reed beds (Phragmites communis), with occasional reports of nests in shrubs in upland habitat regarded as anomalous. Catchpole described a population in which only 54% of all nests were in Phragmites, 26% were in other marsh vegetation, and the remainder were in upland cover. Over a three-year period the portion of territories

in Phragmites declined from 55% to 47% to 41%. Breeding rates and success were alike between marsh and upland habitats, though predation was significantly greater among Phragmites nests. Sixty-five percent of the birds studied by Catchpole nested in habitats different from that of their parents, and two young which were known to be moved as fledglings from Phragmites to upland vegetation later nested in upland habitat. Catchpole's careful analysis of earlier literature on the Reed Warbler suggested that for at least a century the species has not been confined to Phragmites beds. Either the Reed Warbler always has been more flexible in nest site requirements than generally believed, or for a long time it has been diversifying its habitat requirements. Hildén described a number of cases of significant, and in some instances remarkably swift, changes in nest site selection by various species of birds.

Song Posts

Songbirds of most species sing from perches either elevated above most of the surrounding vegetation or at least providing a view of much of the territory and an opportunity for the song to carry some distance. Song posts have been suggested as critical in habitat selection for a wide variety of species (see Kendeigh 1945), but unfortunately little conclusive evidence is available because most species of songbirds nest in variously wooded habitats that provide numerous potential song posts. Many prairie and tundra species have evolved aerial song displays making song posts unimportant. Some such species, however, must have song perches or posts upon which to land after an aerial display. Examples include the Meadow Pipit (Lack 1933, 1937), Tree Pipit (Barruel 1957), Dickcissel (Zimmerman 1971), and Short-billed Marsh Wren (Verner unpubl.). Otherwise unsuitable habitats may be made acceptable with the placement of fences or power poles across the landscape or by placing sticks in the ground specifically for that purpose.

Shelter

Protection from predators and/or adverse weather is obviously vital to birds and is apparently a key factor in habitat selection by some species. Klomp (1954) concluded that Lapwings avoided habitats with trees because they could readily drive away crows approaching on wing but could not effectively defend their nests if trees were available for crows to perch in. Haartman (1960) and Hildén felt the same phenomenon explained the absence of gull and tern colonies from islets on which even a few trees grow. Cullen (1957) provided

extensive documentation of the impact of nest predators on gull behavior and nest site selection, based on his studies of the Kittiwake. The importance of forbs in habitat selection by Dickcissels, Bobolinks, and Lark Buntings has been related in all three species to nest placement and the resultant protection from predation and/or weather (Zimmerman 1966, 1971; Martin 1971; and Shane 1974, respectively).

General Features of Terrain and Vegetation

Many studies indicate that habitat selection by many bird species depends on non-specific stimuli associated with terrain (sloping, flat, undulating, etc.) and/or vegetation (height, density, color, volume) (e.g. see Hildén 1965, Wiens 1969). Cardinals select areas of dense shrubs and vines (Dow 1968, Anderson and Shugart 1974). According to Sturman (1968) the features to which Chestnut-backed Chickadees in Washington State responded were "the percent of the upper story canopy volume which is coniferous and the average height of the upper story conifers." Black-capped Chickadees in Washington selected on the basis of "the canopy volume of all trees, all bushes, and middle story trees together." Zimmerman (1971) found total volume of herbaceous vegetation to be a primary factor in habitat selection by Dickcissels. Studies such as these, taken together with demonstrated correlations between bird species diversity and foliage height diversity and/or percent vegetation cover (e.g. MacArthur and MacArthur 1961; Cody 1968, 1974; Recher 1969; Willson 1974; Balda, this symposium), suggest that birds often respond to the general structure of vegetation rather than to the plant species comprising it.

Other Factors

Many additional features important in survival and reproduction of various bird species have been implicated as factors in habitat selection. Included in this list are water (for drinking), nesting materials, other species of animals, light intensity, soil moisture, vagaries of substrate (e.g. presence and/or size of pebbles), watch-posts for insect-hawking species, and depth of water for some aquatic birds. Data presented here thus far generally demonstrate a great range of variability among bird species with respect to habitat selection. The data also show that for nearly all species our knowledge of specific factors eliciting positive habitat selection responses is woefully meagre. While I believe we must continue to research this problem on a species-by-species basis, I suggest that this is not the most fruitful approach to the immediate problem of managing wild lands in a

manner that will minimize detrimental effects on populations of nongame birds. Studies most likely to yield information widely applicable in habitat management are integrative, multivariate analyses of bird species abundance and habitat variables. For example, Anderson and Shugart (1974) analyzed 28 habitat variables and abundances of 28 bird species in a deciduous forest in eastern Tennessee. James (1971) undertook a similar analysis of 15 environmental variables in the breeding territories of 46 bird species in Arkansas. These two studies elucidated many factors of primary importance in habitat selection by different species. They provide a good baseline for predicting the impact of habitat manipulations on various populations. Comparable studies in North American grassland habitats have been reported by Wiens (1969, 1973), and these can serve as a base for assessing effects of range management practices on bird populations.

Development of Habitat Selection

Habitat management practices must be profoundly influenced by the flexibility of habitat selection by any species. If the stimulus-response system is innate and tightly canalized, even slight changes in habitat may result in local extinction. Habitat selection might be innate but not so tightly canalized, so that early experience could alter later selection of breeding sites, roosting sites, etc. Finally, habitat selection may be largely a result of a bird's experience, so that human modification of natural environments commonly results only in alterations of the preferred habitat of a species. This question has been explored by Hildén through a summary of published field studies, and by Klopfer (1963, 1965, 1967) and Klopfer and Hailman (1965) through experimentation with caged birds. As one might expect, available evidence points to a range among species with respect to the relative roles of experience and inheritance in development of this behavior.

Many authors (e.g. Lack 1933, 1937, 1940; Lack and Venables 1939; Miller 1942; Peitzmeier 1942; Stresemann 1943; Svårdson 1949; and especially Hildén 1965) believe inheritance has a primary role in habitat selection. Evidence cited usually takes the form of species failing to select as breeding sites habitats which, in the field observer's judgment, differ in some small way from the preferred habitat but provide all the requisites for successful reproduction. Such observations support the view that habitat selection has an innate component but in no way conclusively prove it. Experimentation is needed. Newton (1967) examined the roles of morphology and experience in seed

selection by some British finches. He found both related to flexibility in habitat selection by birds in response to human alteration of environments. Young of various species were presented with the same range of food items, differing in size and appearance. All attempted to deal with them in similar ways. However, each individual eventually developed a preference for those foods it could handle most efficiently with its particular morphology and behavior. Thus both experience and inheritance contributed to development of feeding preferences.

Studies like those of Klopfer (1963, 1965, 1967) should eventually put us on firmer ground for interpreting the relative contributions of inheritance and experience in habitat selection. Klopfer has hand-reared Chipping Sparrows in various experimental conditions and found that birds inexperienced with any foliage types exhibited a significant preference for pine foliage over oak foliage. Wild-trapped adults exhibited a similar preference. Hand-reared birds exposed only to oak foliage were later less discriminating in their selection of the foliage type in which they spent most of their time. Klopfer concluded that the Chipping Sparrows exhibited an innate preference for pine foliage which could be modified by early experience. Similar studies of some tropical tanagers (Klopfer 1967) indicated that these species were less innately stereotyped in foliage preferences than Chipping Sparrows. They were more markedly influenced by early experience in their later habitat preferences.

Though we have not yet sifted experience from inheritance as contributors to habitat preference, the fact that a great many species are flexible in their choices of habitats for breeding, feeding, and roosting is firmly established by field studies. This fact is of major importance in habitat management, as it implies that human manipulation of habitats need not preclude their continued utilization by birds. Experience shows us, however, that the more drastic the change, the fewer species can tolerate it. Common Nighthawks have taken to nesting on flat, gravelled roofs. Chimney Swifts have largely abandoned their hollow tree nesting sites to nest, instead, in chimneys; but Vaux's Swifts have not yet done so to my knowledge. Hildén reviewed many instances in which species expanded into habitats formerly non-existent or at least not exploited. Beginning about 1925, the Mistle Thrush in Germany slowly expanded its range from continuous forests dominated by conifers, first into small, cultivated patches of trees with fewer conifers. These were remote from human settlements. Next the thrushes began to breed in trees about farmhouses, and finally they spread into the parks of cities. The Curlew in Germany formerly

avoided tilled lands, nesting instead in their preferred bog habitats. When bogs occupied by breeding Curlews were drained, former inhabitants returned to the same geographic region and nested in the tilled lands. Thereafter the population expanded and spread over tilled lands previously avoided by the species. These are not isolated cases but represent, instead, a fairly common phenomenon in avian biology. They usually are explained as a result of the combined effects of site tenacity (the common tendency of adults to return to breed in their former breeding territory) and the role of early experience on development of habitat selection (young reared in an atypical habitat may later select that sort of habitat for breeding). If individuals which react in these ways reproduce successfully in the new environment, their population should spread rapidly over that environment.

Application of this phenomenon to habitat management may have some promise. For example, Drost (1955, 1958) transported about 1000 Herring Gulls from the German coast to the interior, where they were reared in a zoo. In their first fall, the young gulls dispersed from the zoo. Many returned to the zoo and its surrounding area three to four years later, when they were sexually mature, and nested or attempted to nest. Others settled inland at sites up to 520 km from the point of rearing, and still others nested with coastal populations. A more lengthy discussion of site tenacity and habitat stability, as they influence colonization of new areas, is presented by McNicholl (1975).

Management Implications

The generally inadequate state of our knowledge about specifics of habitat selection by most species of birds need not impede significant progress in formulating management practices to minimize human impact on nongame birds. In the first place, most bird species exhibit some flexibility in their habitat preferences and many species adjust to marked changes in environment. In the second place, common sense tells us that survival and reproduction of any bird species implies adequate food, shelter, nesting sites, song perches, etc. Mere cognizance of the need to manage habitats in a manner favoring bird populations probably will do as much as, or more than, accumulation of a catalog of factors important in habitat selection. Information currently available should be exploited. For example, providing artificial song posts in prairie habitat or nest boxes in woodlands and forest edge may have substantial, positive effects on breeding populations of such species as Dickcissels, Lark Buntings, Short-billed Marsh Wrens, House Wrens, and bluebirds. Research

should continue in the area of habitat selection, but management practices cannot wait until all the results are tabulated.

The demonstration that many bird species select habitats on the basis of rather generalized features such as height, density, and overall complexity of the vegetation, suggests at least a reasonable first approach to habitat management. Within the confines of multiple use (which is implied by the fact that habitats are managed), we should strive to enhance the structural complexity of physical and vegetational features of habitats. Wherever possible we should avoid single-species stands of tree or farm crops. Where this is not possible, variety might be enhanced by reducing the area of each monoculture to achieve at least a mosaic of several small monocultures.

Detailed investigation of the relationships among numerous habitat variables and bird populations (as the Wiens, James, Anderson and Shugart studies) should be encouraged. Such investigations will likely provide widely applicable results in a minimum of time.

SUMMARY

This is not a summary in the sense that it condenses all material in the preceding text. Rather it is a condensation and integration of principal recommendations. These are separated here into (1) recommendations immediately applicable to management and (2) recommendations for research on topics vital to improved management.

Management Recommendations

1. Areas of suitable habitat for any species should be as large as possible, since apparently an arithmetic reduction in utilizable space results in a geometric decline in its value as a preserve (Willis 1974).

2. Prairie habitat providing a heterogeneous mosaic of grasses and forbs is more suitable for nongame birds than uniform stands of either. Controlled burning programs provide a means for regulating plant communities of prairie lands.

3. Marsh nesters generally prefer cattail over bulrush and select stands of intermediate stem density over very sparse or very dense stands. Prudent grazing of cattle in marsh habitats, after the nesting season, might be employed as one means for controlling stand density.

4. Birds of upland shrub and forest habitats respond to general features of vege-

tation height profile, percent vegetation cover, and/or total volume of vegetation. Management of these habitats ought to be geared to enhance the structural complexity of their physical and vegetational features.

5. Every effort must be made to avoid single-species plant communities, or at least to reduce monocultures to small, intermingled patches to achieve a mosaic of monocultures.

6. What little knowledge we have of proximate and ultimate factors important in habitat selection should be applied, as in the provision of artificial song posts for prairie birds and nest boxes for cavity nesters which do not excavate their own nest cavities.

7. Maximum advantage ought to be made of plantings along highways and bordering agricultural lands to provide nesting cover, as breeding density of many species is significantly higher in such belts of habitat than in more extensive patches of suitable cover.

8. Last, and probably most important, a common sense approach to management must prevail against the pressures of human population expansion, as it alone will remind us that we simply cannot alter environments too much without forcing local extinction of most endemic wildlife.

Identified Research Needs

1. Presently no information is available on the minimum number of breeding pairs required to maintain any population. Nor do we know the smallest area of suitable habitat essential to support that number of breeding pairs.

2. Mobility between isolated patches of suitable habitat is necessary for replacement of local extinctions. A totally untapped area of research involves the optimum dispersion pattern of 'habitat islands' conducive to rapid replacement when local extinction occurs.

3. Management would be simplified if one, or perhaps just a few, bird species populations could be monitored regularly as indicators of the suitability of habitats for birds in general. Likely target species should be researched among larger carnivores (hawks, owls, larger insectivores), as they have larger territories, depend for food on lower trophic levels, and apparently are the first to react negatively to accumulation of harmful chemicals in their environment.

4. Research should continue in the identification of proximate and ultimate factors involved in habitat selection by birds. It is

inferred in studies of polygynous species that habitat suitability is correlated with pairing success of males and with the order in which males in a population become paired. The latter procedure may be a valid means for assessing habitat suitability in monogamous species as well.

5. Practically no experimental work is available on the roles of inheritance and experience in development of habitat selection responses among birds. This information is vital to management, since it pertains to the flexibility of birds as they respond to changes in their habitats. Both field and laboratory approaches have been applied successfully to this problem, but on a very limited scale.

6. Finally, research likely to yield maximum applicability in the shortest time is multivariate analysis of many habitat features and all bird populations in specific ecosystems.

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APPENDIX - Scientific names of birds

White Pelican.....Pelecanus erythrorhynchos
 Red-tailed Hawk.....Buteo jamaicensis
 Red-shouldered Hawk.....Buteo lineatus
 Golden Eagle.....Aquila chrysaetos
 Bald Eagle.....Haliaeetus leucocephalus
 American Kestrel.....Falco sparverius
 Red Grouse.....Lagopus scoticus
 Tasmanian Native Hen.....Tribonyx mortierii
 Oystercatcher.....Haematopus ostralegus
 Lapwing.....V. vanellus
 Golden Plover.....Pluvialis dominica
 Black-bellied Plover.....Pluvialis squatarola
 Dunlin.....Calidris alpina
 Curlew.....Numenius arquata
 Herring Gull.....Larus argentatus
 Ring-billed Gull.....Larus delawarensis
 Kittiwake.....Rissa tridactyla
 Caspian Tern.....Hydroprogne caspia
 Cassin's Auklet.....Ptychoramphus aleuticus
 Great Horned Owl.....Bubo virginianus
 Barred Owl.....Strix varia
 Elf Owl.....Micrathene whitneyi
 Common Nighthawk.....Chordeiles minor
 Chimney Swift.....Chaetura pelagica
 Vaux's Swift.....Chaetura vauxi
 Rufous Hummingbird.....Selasphorus rufus
 Allen's Hummingbird.....Selasphorus sasin
 Calliope Hummingbird.....Stellula calliope
 Anna's Hummingbird.....Calypte anna
 Red-bellied Woodpecker.....Centurus carolinus
 Golden-fronted Woodpecker.....Centurus aurifrons
 Western Kingbird.....Tyrannus verticalis
 Cassin's Kingbird.....Tyrannus vociferans
 Great Crested Flycatcher.....Myiarchus crinitus
 Least Flycatcher.....Empidonax minimus
 Tree Swallow.....Iridoprocne bicolor
 Cliff Swallow.....Petrochelidon pyrrhonota
 Purple Martin.....Progne subis
 Golden Oriole.....O. oriolus
 Australian Magpie.....Gymnorhina tibicen

Great Tit.....Parus major
 Black-capped Chickadee.....Parus atricapillus
 Chestnut-backed Chickadee.....Parus rufescens
 Plain Titmouse.....Parus inornatus
 Bridled Titmouse.....Parus wollweberi
 House Wren.....Troglodytes aedon
 European (Winter) Wren.....T. troglodytes
 Long-billed Marsh Wren...Telmatodytes palustris
 Short-billed Marsh Wren...Cistothorus platensis
 Mistle Thrush.....Turdus viscivorus
 American Robin.....Turdus migratorius
 Eastern Bluebird.....Sialia sialis
 Western Bluebird.....Sialia mexicana
 Mountain Bluebird.....Sialia currucoides
 Reed Warbler.....Acrocephalus scirpaceus
 Blue-gray Gnatcatcher.....Polioptila caerulea
 Goldcrest.....R. regulus
 Ruby-crowned Kinglet.....Regulus calendula
 Pied Flycatcher.....Muscicapa hypoleuca
 Collared Flycatcher.....Muscicapa albicollis
 Meadow Pipit.....Anthus pratensis
 Tree Pipit.....Anthus trivialis
 White Wagtail.....Motacilla alba
 Starling.....Sturnus vulgaris
 Ovenbird.....Seiurus aurocapillus
 American Redstart.....Setophaga ruticilla
 Bobolink.....Dolichonyx oryzivorus
 Eastern Meadowlark.....Sturnella magna
 Western Meadowlark.....Sturnella neglecta
 Yellow-headed Blackbird.....X. xanthocephalus
 Red-winged Blackbird.....Agelaius phoeniceus
 Tricolored Blackbird.....Agelaius tricolor
 Brewer's Blackbird.....Euphagus cyanocephalus
 Common Grackle.....Quiscalus quiscula
 Greenfinch.....C. chloris
 Cardinal.....C. cardinalis
 Dickcissel.....Spiza americana
 Seaside Sparrow.....Ammospiza maritima
 Lark Bunting.....Calamospiza melanocorys
 Chipping Sparrow.....Spizella passerina
 White-throated Sparrow...Zonotrichia albicollis
 Song Sparrow.....Melospiza melodia

Vegetation Structure and Breeding Bird Diversity¹

Russell P. Balda²

Abstract. --Breeding bird communities consist of individual species that select a definable area because of the presence of requirements needed for reproduction. The actual process of habitat selection is complex. The avian community is a result of eons of evolution by both the plants which supply requisites and the birds which must be efficient harvesters of these requisites. Numerous structural components of the community have been found to be of value in predicting bird species diversity. Foliage height diversity appears to be the best factor measured to date but percent cover, foliage volume, plant species diversity, and foliage height are also useful measures from which to predict bird species diversity. The presence or absence of seeds, fruits, and berries are possibly important, but to date have not been fully assessed.

Ecotones created by the interdigitation of successional stages are known to support greater diversity than homogeneous communities, and late successional stages support greater species diversity than earlier stages because of vegetative complexity.

Most studies to date on breeding birds and their vegetative substrate have been correlational and have not measured the components of the plant community used by the breeding birds. Because of this the manager has little idea of what a particular vegetative component of the community provides the breeding birds. Most seral and ecotonal species may have relatively great dispersal potential, wide ranges of tolerance, and high reproductive rates. Birds restricted to climax communities may have relatively low dispersal powers, narrow ranges of tolerance and low reproductive rates. If such is the case, then climax communities may require more attention than presently given them as areas to maintain a select group of bird species with narrow ecological ranges of tolerance.

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INTRODUCTION

An avian community, by definition, is simply an aggregate of species, existing together in some definable area that provides the species specific requirements. Each species is restricted in its habitat selection by various physiological, morphological, psychological and ecological traits. A species can exist only in habitats where these specific requirements are fulfilled (fig. 1). Some species appear to have rather narrow ranges of tolerance for specific factors (stenotopic species such as the Kirtland's Warbler *Dendroica kirtlandii*) and others very broad ranges of tolerance for requisites (eurytopic species such as the Robin, *Turdus migratorius*). Groups of species that function in a similar manner (i. e. ground foraging, leaf gleaning, bark probing, fly-catching, etc.) are referred to as belonging to the same guild (Root 1967).

A voluminous amount of information has been published on birds and their vegetative substrate. Avian ecologists have used at least five different points-of-view in addressing themselves to the problem. These approaches range from intensive autecological studies in which a single species is investigated thoroughly over a period of time in a single or number of habitat types (Root 1967), to a totally synecological approach in which species are simply identified and counted and some (or even one) component of the vegetation is measured. There is a gradation between these opposite extremes as some studies have concentrated on a few birds and on specific features of the habitat. It is important to recognize that different approaches will yield different types of information upon which to base management decisions and some approaches may provide data that are of very little value to land managers. A complete autecological study will provide valuable information for single species (or possibly guild) management but little useful data about managing for optimum community inhabitation. A total synecological approach may indicate some constraints in managing for complexity of the avian community but will not identify the specific species or the specific requisites being provided. Both approaches have certain advantages and disadvantages, but it appears that an approach that links a specific area and its physiogomy to a specific bird or group of birds (guild) would be most beneficial to managers.



Figure 1. --Species specific requirements need to be matched by provisions provided by the habitat for successful inhabitation to occur.

The number of species that a natural, relatively undisturbed plant community will support can vary from one area to the next and also from year to year and most certainly from season to season because of the migratory nature of many birds. Breeding species numbers on three study plots in ponderosa pine (*Pinus ponderosa*) forest varied by as much as 40 percent (Table 1). The only variable that appeared to be important was weather conditions between the two years. The winter of 1973 was harsh and snow melt occurred relatively late, whereas in 1974 the winter was mild and dry.

The number of diversity of species in similar plant communities may also vary because of a constellation of factors including latitudinal differences, geologic age of the particular habitat type (Darlington 1961), restrictions on colonization of the area (i. e.

Table 1. --Numbers of Breeding Species on Three Ponderosa Pine Study Plots on the Beaver Creek Watershed, Flagstaff, Arizona¹

Study Plot	Number of Species		
	1973	1974	Differences (%)
A	13	16	3 (18.75)
B	16	22	6 (27.27)
C	12	20	8 (40.00)

¹ Data from Szaro and Balda, unpublished.

Wiens 1974) and many others (Pianka 1966). Techniques for counting the number of species also vary from an actual count on a set grid (spot map method - Williams 1936; Kendeigh 1944) to a transect method where densities are calculated based on the conspicuousness of the species (Emlen 1971). Census takers also vary in their powers of audio and visual observation. These complications make it extremely difficult to state with any degree of confidence how many species of birds should breed in a given habitat type at any one point in time (fig. 2). This figure indicates that in general bird species numbers increase as the complexity of the vegetation increases; but, although the trend is obvious, the scatter within habitats varies considerably.

Similarly, the populations of many species show rather dramatic fluctuations from one year to the next even when the vegetative habitat is not physically modified. Many times fluctuations in densities reflect conditions either not related to habitat modification (i. e. winter climate) or conditions on the wintering grounds (Fretwell 1972). Breeding densities between years varied by as much as 80 percent for some species (Table 2) on study plots in ponderosa pine forests that were not physically altered between breeding seasons.

One can look at the number of species and community densities as being controlled by factors that gradually grade from what I refer to as "habitat independent variables" to totally "habitat dependent variables" (fig. 3). Physical factors and seasonal events can influence the number of species and possibly the densities that can exist within a particular plant community. The most important factors, however,

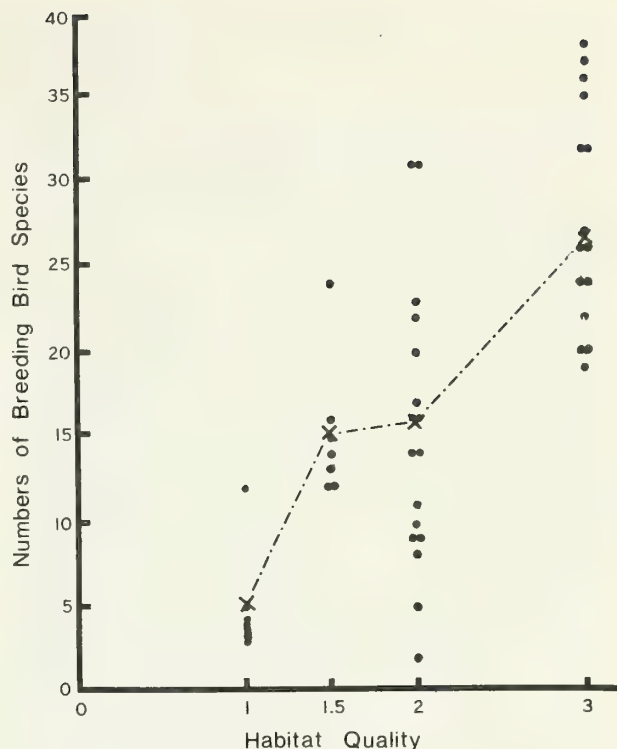
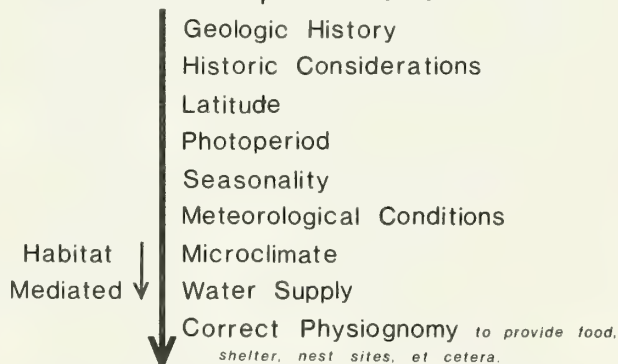


Figure 2. --The relationship between habitat quality and the number of breeding species in the community. Habitat quality is based on the number of vegetative strata: 1. grassland, shrub-steppe; 1.5 chaparral; 2. Sonoran desert, pinyon-juniper woodland, ponderosa pine forest; 3. deciduous forest, mixed coniferous forest. (Data from various sources)

Habitat Independent Variables



Habitat Dependent Variables

Figure 3. --Variables that are relatively independent of the foliage configuration grade and combine with habitat dependent variables to control bird species diversity within a given community.

Table 2. --Densities of Selected Breeding Birds Between Years in a Ponderosa Pine Forest¹

Species	Pairs per 100 Acres		Differences (%)
	1973	1974	
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	4.50	9.00	4.50 (50.00)
Western Bluebird (<i>Sialia mexicana</i>)	6.75	12.00	5.25 (43.75)
Broad-tailed Hummingbird (<i>Selasphorus platyceris</i>)	3.00	15.00	12.00 (80.00)
Solitary Vireo (<i>Vireo solitarius</i>)	6.00	12.00	6.00 (50.00)
Chipping Sparrow (<i>Spizella passerina</i>)	4.50	12.00	7.50 (62.50)
Rock Wren (<i>Salpinctes obsoletus</i>)	3.75	8.25	4.50 (54.55)
Gray-headed Junco (<i>Junco caniceps</i>)	6.00	10.50	4.50 (42.86)
Grace's Warbler (<i>Dendroica graciae</i>)	7.50	18.75	11.25 (60.00)

¹ Data from Szaro and Balda (unpublished).

are termed proximate factors (Hilden 1965) and are habitat dependent. Habitat selection can be viewed as a system designed to provide the species with all requisites for survival and reproduction. These requisites, termed ultimate factors (after Baker 1938), encompass food, shelter, and correct physiogomy (Hilden 1965). The factors that serve as initial attractants to the birds may be almost irrelevant to the bird *per se* but serve in some way as reliable indicators of the bird's probability of success because the area is suitable for breeding. These factors may include landscape and terrain, stimuli from nest sites, song posts, feeding and drinking sites, food, and possibly other animals. If Hilden's ideas are correct, and there seems to be considerable supporting evidence for them, then our problems of identifying what structural features of the habitat are selected by birds are increased to where it is necessary to make species specific assessments. Lack (1933) was first to show that on successional areas where rapid revegetation is occurring, a drastic change in avifauna can occur in a relatively short time. On a heath land replaced by pines an entire new avifauna replaced the original in five short years. The two most important factors were suitable nesting requirements and a correct set of psychological characters. For example, the Tree Pipit

(*Anthus trivialis*) and Yellow Warbler (*Phylloscopus trochilus*) did not inhabit areas when large trees or bushes were absent even though they were used only for courtship. An important psychological factor appears to be height of the vegetation, irrespective of the use of these heights for nesting or feeding. Lack stressed the psychological aspects of habitat selection (proximate factors of Hilden 1965) rather than the ultimate factors. The fact that there are both habitat independent factors and psychological factors operating on the size and complexity of the avian community suggests it is not extremely wise or desirable to base management decisions on information generated from distant geographic localities, or from abbreviated or short term studies.

SPECIES DIVERSITY

Because biotic communities are the end result of eons of evolutionary history one would expect that selective pressures such as predation, competition, and coevolution may play some role to mold avian communities into a type of organization that would reflect efficient use of the available resources (Margalef 1963). One of the measurable characteristics of this organization is the diversity of bird species that inhabit the plant communities. This within-habitat diversity is referred to as

"alpha" diversity by Whitaker (1965) who correctly recognized a number of different types of diversity.

Although a number of mathematical measures exist to determine an index of diversity, the most popular and widespread one in use by avian ecologists is the Shannon formula (Shannon and Weaver 1963):

$$H' = \sum_{n=1}^s p_i \log p_i$$

This formula takes into account two components of each entity (species) in the community: (a) the presence of each species or the sum total of all species in the community, often referred to as the species richness component, and (b) the relative abundance (p_i) or the proportionality of each species in the community which is referred to as the equitability component (Lloyd and Ghelardi 1964; Pielou 1966). High H' values (indicating greater diversity) are obtained in cases where more species are present (greater richness) and/or where the individuals are more evenly distributed among the species (equitability). H' has some qualities which make it intuitively attractive as an index of species diversity. Because H' is dependent upon richness and equitability, one often asks how a particular H' is related to the maximum H' . Maximum H' (H'_{\max}) is simply the $\log N$ where N is the number of species in the community. At H'_{\max} all species are represented by the same proportion of individuals. In a four species community, for example, each species contributes 25 percent of the individuals, and in a three species community each contributes 33 percent. The H' for the four species community arranged as above will be higher than that for the three species community. According to Pielou (1966) a measure of evenness (J') can simply be calculated as $J' = \frac{H'}{H'_{\max}}$.

This value varies from 0 to 1, where all species have equal densities. If we take $e^{H'}$ we get the number of equally common species or equally dense strata of vegetation (E) for our sample (MacArthur 1964). Unless H' equals H'_{\max} , E will always be less than the number of species present because rare species contribute less than common species. The strengths, weaknesses, uses, and ecological and evolutionary implications of this and other measures of diversity are discussed in detail by MacArthur (1965, 1972), Pielou

(1969), Hurlbert (1971), DeBenedictis (1973) and Peet (1974).

In many cases the correlation between bird species diversity and species richness is so high it is possible to simply use the number of species as an index (Tramer 1969).

FOLIAGE HEIGHT DIVERSITY

In 1961 MacArthur and MacArthur published a classic report on the relationship of bird species diversity to vegetation complexity. They showed an extremely strong correlation of bird species diversity (BSD) with foliage height diversity (FHD). The latter factor was determined by an indirect measurement of the amount of leaf surface area present in horizontal layers above the ground. MacArthur and Horn (1969) present a simple technique for calculating a foliage profile for a forest. MacArthur and MacArthur (1961) report that when the foliage is divided into three horizontal layers 0-2 ft, 2-25 ft, and above 25 ft, and the FHD calculated, a very close fit of BSD and FHD resulted. They indicate that a similar increase in BSD will result with the addition of any one of the layers regardless of which layer is present or which is added. Thus each layer is of equal importance. The authors found that although plant species diversity (PSD) may be a good index of BSD, once FHD has been calculated nothing can be gained by adding PSD. They conclude that if the horizontal bands of foliage are diverse (have high equitability) then BSD will be high regardless of PSD. Birds may be responding to the patchiness of the forest as arranged on a horizontal scale. Additional data presented by MacArthur, et al. (1962) indicated that in bushy fields and early successional stages specific bird species and their densities can be predicted from measurements on the amount of patchiness of the habitat which in essence is foliage diversity within only two strata. MacArthur (1964), working in complicated woodlands and succulent Sonoran Desert, was able to extend their earlier conclusions about the relationship of FHD to BSD. He did point out, however, that he could not predict the actual species that were present and that other factors, such as the presence of water or nesting holes, may also be important dimensions which need be incorporated to predict BSD.

Because this method appears to be the simplest, most straight forward, easiest to

use, and presently the most popular, I will compare other findings to results predicted from FHD.

STRUCTURALLY SIMPLE HABITATS

Studies done in less complex habitats have also confirmed the relationship between BSD and FHD. Cody (1968), working in grassland habitats where little opportunity for vertical habitat selection exists, attempted (among other things) to determine what plant characteristics are important in determining BSD. He found that the species overlapped broadly in their breeding territories. Thus inter-specific territoriality played no role in habitat selection (i. e. specific patches were not being selected) and a finer subdivision of the habitat was occurring. He concluded that the number of bird species existing in any grassland can be predicted from the mean height of the grass and its standard deviation. This model assumes that all grassland habitats are saturated with bird species. The prediction is shown to hold regardless of bird or plant species composition. The avian community in grasslands is organized by one of its most obvious structural features, grass height.

Wiens (1969) measured numerous variables found in a grassland habitat, and linked these variables to the specific territories of seven breeding birds and to their behavior. He found that each species differed from the others in one or more features of habitat occupancy, but some of these differences were slight. The most obvious differences between species were in density and height of the vegetation on the territories, but amount of litter, forb density, height, structure and presence or absence of trees also played a role. He was able to rank seven breeding species on a gradient of habitat "quality" based on the above measures. Wiens (1969) methodology is worth noting here as he put the problem of habitat selection based on vegetational characteristics into proper perspective by relating to specific bird species. Community dynamics can be profitably studied using this approach.

Avian communities in North American Desert habitats may not be arranged as predicted by the FHD when calculated from three horizontal bands of vegetation as used in forest and woodlands. Austin (1970) in the Mohave Desert found a good correlation between BSD and FHD after he divided the foliage into hori-

zontal bands of zero to 3 ft, 3 to 6 ft, and above 6 ft. His data show that desert birds appear to recognize between 1.5 and 2.5 equally important dimensions indicating the breeding birds respond appropriately to the real habitat they inhabit. This holds though many if not most desert species do not utilize creosote-bush (*Larrea tridentata*), an important component of the vegetation. Raitt and Maze (1969) concluded Chihuahuan Desert habitats have a complex physiogomy because of the relatively simple layering of the vegetation but a relatively great amount of diversity of life forms of vegetation.

ECOTONES AND SUCCESSIONAL STAGES

Obviously, if BSD can be predicted from FHD then successional stages of a plant association should show a progressive increase in bird species. Kendeigh's (1946) results from mixed-deciduous forests demonstrate this relationship (fig. 4) as does the work of Beecher (1942) and Johnston and Odum (1956). This is so because specific species (edge species) are often attracted to ecotones and supplement

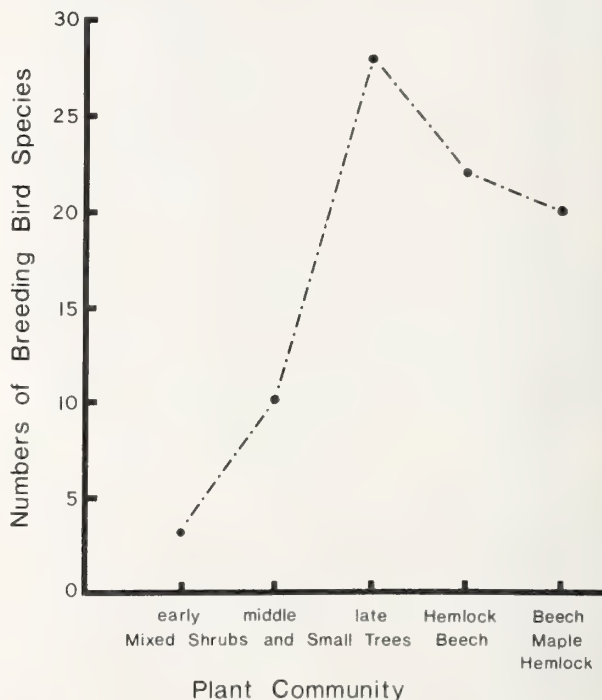


Figure 4. --Relationship between number of breeding species and successional stages of a mixed deciduous forest. Data from Kendeigh (1946).

the birds from each major community which inhabit these edges. Kendeigh (1948) found that the ecotone between deciduous and coniferous forest in Michigan supported the greatest diversity of bird species.

Karr (1968), studying succession on strip-mined areas in Illinois, showed that species composition and density increased from bare ground through shrub stages to bottom land forest and then decreased in the climax. Karr (1968) measured FHD, category diversity (plant species, bare ground, water etc.) and plant species diversity on his study areas. In the four successional areas studied only FHD showed a linear relationship with BSD. Margalef (1958, 1963) also suggests that diversity should increase through earlier successional stages and then decrease in stages approaching the climax. Karr also showed that available water may act as a partial layer of foliage, and that a straight line relationship exists between BSD and the logarithm of percent vegetation cover.

Shugart and James (1973) found that upland succession in Arkansas involved three general habitat types, fields of grasses and forbs, fields of shrubs and shade intolerant trees, and forests. Each has a distinct composition of breeding birds. Bird densities and diversities increased with the relative age of the community which is most likely related to the increased complexity of the plant community and increased foliage height.

Little work has been done on the permanent ecotones that exist between plant communities in the mountainous areas of southwestern U.S. where ecotones are narrow bands because of abrupt elevational changes. A recent study (Laudenslayer and Balda, MS) found that in a ponderosa pine-pinyon pine (Pinus edulis)-juniper (Juniperus spp) ecotone, the number of breeding species (5) was lower than in either of the two communities flanking it and had a diversity similar to that of grasslands (Cody 1966). The foliage was obviously more complex than either contributing community. The apparent reason for this is believed related to the lack of birds using the ponderosa pines and especially the higher reaches of these pines even by the birds that normally inhabit the ponderosa pine forest. It is distinctly possible that the permanent ecotones (transition zones) between plant associations do not support higher BSD than the contributing plant communities. In the montane

southwest there appear to be few if any truly ecotonal plants or birds that inhabit this type of ecotone. In the ecotone studied by Laudenslayer and Balda (MS) 10 percent of the foliage of ponderosa pine was located between 9 and 20 m off the ground. This broad segment of vegetation was not used by the breeding birds. If one is to use some measure of vegetation to explain BSD the measure should consider parameters within the plant community that are being used by the birds.

The above studies indicate beyond doubt that the complexity of the vegetation plays an important role in determining BSD and there is convincing evidence to suggest that FHD is the component around which avian communities are organized. The biological significance of these findings, however, has eluded us because few of the above studies actually linked birds to their strata or how each species or ecologically similar species (guilds) respond to the complexity of the vegetation.

OTHER SPECIFIC FACTORS

A number of studies have been published which suggest that some factor other than FHD may be important in determining BSD. In some cases FHD has not served as a good measure of BSD.

Balda (1969) could find no correlation between FHD and BSD when comparing a ponderosa pine forest and an oak-juniper-pine woodland in southeastern Arizona. Because actual foliage volumes for trees and shrubs and saplings were measured as well as bird heights and activities in the trees it was possible to compare community bird use of each plant type. Assuming that birds of a community will use each plant type in proportion to its availability it is then possible to determine how important a particular plant species may be to the bird community. Table 3 indicates that although Juniperus deppeana is the most dense tree in the community it is used far less than expected. This may be an important explanation for the lack of correlation between FHD and BSD. Junipers appear to be spreading rapidly through the lower elevations of the southwestern desert mountains. Numerous hypotheses have been put forth to explain this encroachment (Marshall 1957; Humphrey 1962) but the effects on the avian community have not been investigated. The tree species that form the long standing

plant community, the oaks and pines, were overused, which may indicate that recency of appearance by the juniper may be the reason it is underused. The birds of this particular community may not have learned or be

vegetation and the avian community but also asked more specific questions about the actual species and their interrelationships with each other and the vegetation. She found that BSD was correlated with FHD except in areas with

Table 3. --Bird-Foliage Relationships in an Oak-Juniper-Pine Woodland in Southeastern Arizona¹

Tree Species	Relative Dominance	Foliage Volume ²	Expected Bird Use ³	Observed Bird Use
<u>Juniperus deppeana</u>	60.1	113,551	495	144
<u>Pinus leiophylla</u>	18.2	39,985	150	297
<u>Quercus spp</u>	21.3	38,986	175	338
<u>Pinus cembroides</u>	0.4	1,234	3	44

¹ Portion of data from Balda (1969).

² ft³ per acre of foliage volume.

³ Based on proportions of foliage available and 823 bird observations.

morphologically equipped to make efficient use of it. In north-central Arizona where juniper may have a long history as a major component of the pinyon-juniper woodland, no avoidance of juniper was noted, and it was used in proportion to its availability by the bird community (Laudenslayer and Balda, MS).

Karr and Roth (1971) found that BSD was linearly related to FHD and sigmoidally related to percent vegetation cover when comparing study areas in Texas, Illinois, and Panama. They also showed that in some cases the amount of foliage volume as measured by cover is a better predictor of BSD than FHD. In grassland areas BSD did not increase as grass cover increased but a steep rise in species diversity occurred when shrubs were added and percent cover was between 80-100 percent. A peak rate of increase occurred when both shrubs and trees were added and cover values are between 100-150 percent. At about 230 percent cover BSD levels off (fig. 5). They and Marshall (1957) suggest that at higher densities of vegetation cover BSD will actually decline because the numerous species that must maneuver in and between trees will be restricted in mobility by the dense foliage. This may quite possibly be the reason some climax communities have a lower BSD than do some intermediate successional stages.

Willson (1974) was not only interested in the relationship between complexity of the

large trees, where no correlation was evident. This is in contrast to the earlier findings of MacArthur and MacArthur (1961). Percent vegetation cover also was nonlinearly correlated with BSD showing the greatest increase where both shrubs and trees were present and the cover between 140 and 160 percent.

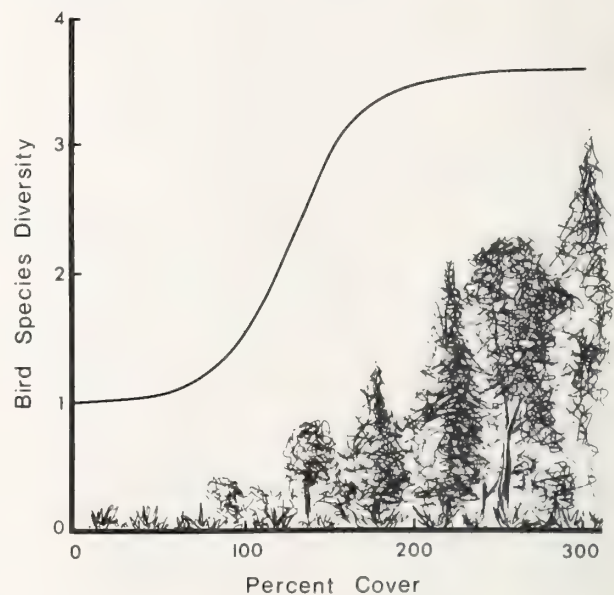


Figure 5. --Relationship between percent cover of herb, shrub, and tree layers to bird species diversity. (Data from Karr and Roth, 1971).

Once the middle and upper layers of vegetation reached about 50 percent plant cover no additional species invaded the area. The increase in species is directly related to an increase in the number of different guilds that can utilize the area rather than an expansion of guilds already present. Her guilds, however, were very finely defined and in some cases a guild may be no more than one or two species. In her conclusion Willson (1974) questions not only the overall validity of using FHD as a predictor of BSD, but the biological justification for doing so: "We probably should be hard pressed to justify measuring FHD for the prediction of BSD, when we do not really know what that means." At least some measure of cover or foliage volume gives an index of potentially available resources, whereas FHD simply measures the quantity of foliage per arbitrarily defined strata. These strata, as defined by MacArthur and his coworkers, may or may not be of biological importance to the birds.

Using bird data and foliage data from tropical habitats, MacArthur et al. (1966) found that when BSD was regressed in FHD, residual scatter was minimized when the authors used two layers of vegetation for Puerto Rican birds and four layers for Panamanian birds. Thus the former collection of species act as if the habitat is subdivided rather coarsely, whereas the latter habitat is more finely divided. Because no data on bird use (or avoidance) of portions of the habitat is provided it is difficult to accept or reject their hypothesis. Karr (1971) found that FHD "underestimates" the change in bird species diversity in tropical forests. The addition of fruit eaters (frugivores) added an important additional group of birds. The addition of fruit to the habitat added an important dimension that was not accounted for by foliage configuration.

In a ponderosa pine forest plot total foliage volume was reduced by 18 percent by timber harvest yet there was no change in FHD. This occurred because all height classes remained and there was no change in the proportion of foliage present per height class (Szaro and Balda, unpublished data).

Carothers et al. (1974) studied bird populations in riparian habitats in north-central Arizona that support cottonwood (Populus fremontii) and mixed deciduous woodlands. BSD was similar on all plots yet FHD

was much higher on the mixed deciduous areas. Reasons for this difference appear related directly to the small strip of vegetation they studied. Adjacent to the heavily populated cottonwood areas were agricultural lands that possibly had a high, but unutilized standing crop of food. Only 36 percent of the birds in the cottonwood woodlands foraged exclusively on their territories, the remainder spent considerable time harvesting the unused resource in the fields. In contrast, 57 percent of the birds of the mixed deciduous woodlands used their territories extensively to feed. The avian communities were structured differently and this arrangement resulted in a very different relationship between existing foliage and nesting bird densities.

Another problem is additional plant variables often not measured. Working at one level of discrimination we may measure the density and dominance of pinyon pine in a pinyon-juniper woodland but for some species the presence and productive history of pinyon pine cones and seeds may be the important factor to maintain populations of Piñon Jays (Gymnorhinus cyanocephalus) (Balda and Bateman 1971, 1972) and Clark's Nutcracker (Nucifraga columbiana) (Vander Wall and Balda MS). Both species may become nomadic in years when cone crops fail and depart their usual home ranges. In years when cone production is high the former species may be very dense in local areas. Consequently, H' actually decreases because the area is monopolized by one species whereas other species may maintain their usual densities.

The densities of wintering Townsend's Solitaires (Myadestes townsendi) in the pinyon-juniper woodland appears directly related to the density of juniper berries present in the area (Salmonson and Balda, unpublished data). Thus, seeds and berries may be important characteristics of the vegetation that are overlooked when vegetational characteristics are measured.

Birds normally establish their territories and commence advertising for mates in the deciduous forest before the foliage has completely leafed out. Maybe a better fit between BSD and FHD would result if all foliage measurements were taken at the time of territorial establishment when the actual process of habitat selection is underway.

An interesting contrast occurs in the oak woodlands of southeastern Arizona pre-

dominated by "live" oaks, so called because they retain their leaves throughout the winter months. Leaf fall, however, may be complete by late April and early May after many birds have established territories. The net result is that many early arriving foliage nesters desert their territories and later arrivals may not establish territories in the area. Thus, the avian community contains a relatively low proportion of foliage nesting species and a high proportion of species that nest in shrubs, succulents, and in cavities. Therefore, the phenology of the dominant plants may play an important role in habitat selection and the composition of the breeding bird community (Balda 1970).

PLANT SPECIES DIVERSITY

Although MacArthur and MacArthur (1961) state that plant species diversity (PSD) may be a good indicator of BSD they give no data to confirm this statement. Karr (1968) had a strong correlation between the two on his bare ground and shrub stages but the relationship did not hold for the bottomland forest, a late successional stage.

BSD was compared to PSD (including trees, shrubs, and succulents) for seven study plots in the Chiricahua Mountains of south-eastern Arizona (Balda 1967). A significant correlation resulted when the relative densities of the plants were used (fig. 6). Because of the way measurements were taken by the MacArthurs and the nature of the data, their slope is much steeper but, nonetheless, PSD can be used in some cases as an indicator of BSD.

Tomoff (1974) measured plant densities, FHD and physiognomic coverage diversity (PCD) in an attempt to relate BSD to some measure of vegetative complexity. FHD failed to predict BSD when the foliage was divided into zero to one m, 1-2 m and above 2 m. However, when PCD (described as a simplified scheme of life forms divided into categories) was used a significant relationship resulted. Tomoff (1974) concludes that plant species diversity may be highly important in habitat selection by desert breeding birds because each plant species may have discrete properties which act to supply nesting requisites to the breeding birds. In other words, one deciduous tree species may look like any other deciduous tree to a bird selecting a habitat; but such is possibly not the case for desert plants. This may

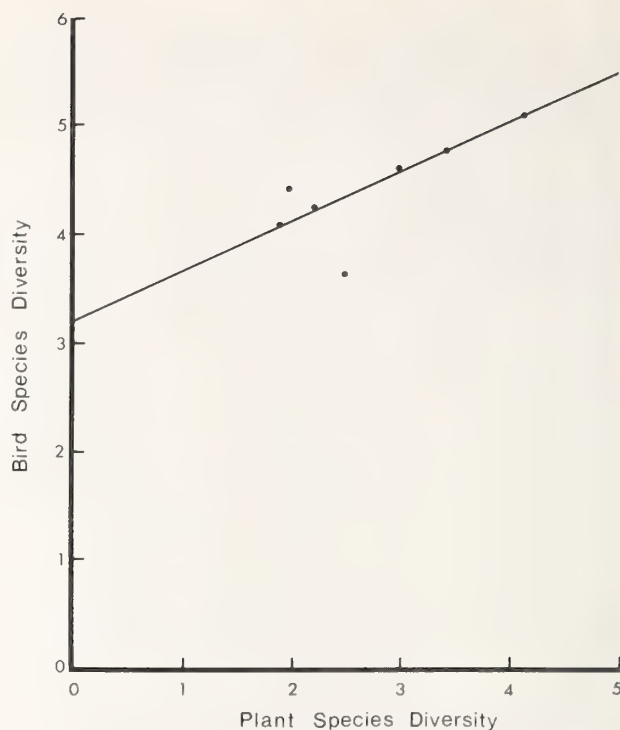


Figure 6. --Relationship of plant species diversity to bird species diversity from seven communities in the Chiricahua Mountains, Arizona. The point below the line is an overgrazed grassland.

be the reason MacArthur and MacArthur (1961) found no improvement in predicting BSD by using PSD once FHD was known.

FOLIAGE VOLUME

The distribution of foliage volume at various heights in trees has been measured and compared to bird use of these strata. Studies by Balda (1969) and Pearson (1971) indicate that in both dry tropical forest and coniferous forest the birds appear to spend more time at the higher reaches of the trees. This is probably a result of a constellation of factors. Birds usually sing from high exposed song perches and may also feed there. Insect productivity is probably greater at the apex where young soft shoots are growing than at the lower reaches. Insects may become active there earlier in the day because of the way sun illuminates and warms the upper portions of the trees. The upper strata of some forests are less dense than lower layers allowing the birds more openings for maneuvering than the lower densely packed areas.

As mentioned previously, numerous studies have indicated a relationship between bird species diversity and height of the vegetation. This may be so because of the factors, especially productivity, mentioned above. If some species are limited by foliage volume and are somewhat restricted to tops of tall trees than silviculture methods that remove the majority of the tall trees may place these species in jeopardy.

SNAGS - AN UNMEASURED VARIABLE

An increasingly important aspect of our forests is the utilization of dead and dying trees for materials and firewood. Scant attention has been paid to these snags in any of the studies reported on herein, yet the secondary cavity nesting guild (those birds that nest in old woodpecker holes and natural cavities) may rely heavily on them for nest and roost sites. It seems plausible that the presence and density of usable snags may play an important role in determining the density and diversity of secondary cavity nesters. A brief analysis of the problem will be presented here to show the importance of measuring habitat variables of significant biological importance to specific members of the avian community in an attempt to determine BSD or some other measure of predictive value. In three ponderosa pine forests undisturbed for at least 60 years the secondary cavity nesters contribute between six and nine species and 56 and 108 breeding pairs per 100 acres. This is about 28 percent of the species and 40 percent of the breeding pairs (Table 4). BSD was extremely close for these areas, only varying between 2.39 and 2.59.

On three adjacent experimental plots on the Beaver Creek Watershed near Flagstaff, three different treatments of snags and oaks were performed. On one area all snags and oaks were removed, on another all snags were removed and on a third oak and pine snags were all left intact. The number of secondary cavity nesting species varied from three in the first mentioned area to seven in the area with all oaks and snags left in place. The percent of all breeding species varied from 19 to 35. The number of breeding pairs varied from a low of 19 to 55 per 100 acres for a change of 65 percent. The percent of all breeding pairs varied from a low of 21 percent to a high of 38 percent, a 45 percent change. BSD of the species of secondary cavity nesters

increased considerably from the snagless plot to the plot with all snags in place (Table 5). This entire nesting guild shows an increase in nesting species, abundance and BSD as the number of snags increases, yet these apparently vital portions of the environment have been ignored in past studies.

What is the significance of the above findings to forest managers? All seven species in Table 5 are insectivorous, but more importantly five of these contributed between 63 and 73 percent of the overwintering individuals in a natural ponderosa pine forest and all five are insectivorous. During the winter, insect densities are obviously low and presumably the birds are eating hibernating adult insects, larvae, and eggs. It is very likely that the wintering birds are exerting more control on the insect populations at this time than they do in the other seasons, as potential breeders are being harvested at this time. Thus, the importance of this nesting guild becomes immediately obvious. Also, if we alter or destroy our climax communities we also destroy the nesting sites of these birds and snagless seral stages do not provide these sites.

SINGLE SPECIES STUDIES

A few studies have been done to relate the structural complexity of the habitat to the actual use of a few or a single species. Sturman (1968) studied the relationship of two species of chickadees, Parus rufescens and Parus atricapillus, to their characteristic habitats at 17 sites. Species densities were determined as well as 32 measures of the vegetation which included: number, diameter, height of the trees, height at which first live foliage was found on a tree, and the number of snags present. For each density a set of independent variables was tested with multiple regression analysis. This method gives a predictive value of the dependent variable (bird density) on the basis of a combination of independent variables as well as adding variables in a stepwise approach which progressively increase the correlation between the bird density and habitat variables. The density of the Chestnut-backed Chickadee was most closely correlated (predicted) by the percentage of the higher reaches of the forest contributed by the coniferous trees and secondly by the average height of the upper story conifers. These two variables accounted for over 90 percent of the variation in abundances. The

Table 4. --Densities of Secondary Cavity Nesters of Three Natural Ponderosa Pine Forests in Arizona (pairs/100 acres)

Species	Location		
	Pearson Natural Area Flagstaff ¹	Watershed 13 Beaver Creek ²	Chiricahua Mts., SE Arizona ³
Pygmy Nuthatch (<i>Sitta pygmaea</i>)	26	15	43
Violet-green Swallow (<i>Tachycineta thalassina</i>)	30	9	3
Mountain Chickadee (<i>Parus gambeli</i>)	20	8	0
Mexican Chickadee (<i>Parus sclateri</i>)	0	0	7
Western Bluebird (<i>Sialia mexicana</i>)	15	6	20
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	7	11	10
Flammulated Owl (<i>Otus flammeolus</i>)	0	0	7
House Wren (<i>Troglodytes aedon</i>)	0	0	10
Pygmy Owl (<i>Glaucidium gnoma</i>)	0	0	1
Western Flycatcher (<i>Empidonax difficilis</i>)	7	7	7
Total Species	6	6	9
Percent of All Breeding Species	26	30	29
Total Breeding Pairs Per 100 Acres	105	56	108
Percent of All Breeding Pairs	45	42	32
H'	2.3938	2.5153	2.5913

¹ Data from Carothers et al. (1973).

² Data from Szaro and Balda (unpublished).

³ Data from Balda (1967).

Black-capped Chickadees density was best predicted when canopy volume of all trees, bushes, and the middle story foliage volume were considered jointly. These three variables accounted for over 90 percent of the variation in abundance. The value of this approach has not been appreciated to date but

can provide valuable management data when properly applied.

Breckenridge (1956) used a single factor approach to determine the most important habitat cue used by Least Flycatchers (*Empidonax minimus*). Although few factors

Table 5. --Densities of Secondary Cavity Nesting Birds on Beaver Creek Watersheds Subjected to Various Snag Removal Treatments (pairs/100 acres)

Species	Watershed Treatments		
	All Snags and Oaks Removed	Oaks Present	Oak and Pine Snags Present
Violet-green Swallow (<i>Tachycineta thalassina</i>)	0	3	9
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	9	9	10
Pygmy Nuthatch (<i>Sitta pygmaea</i>)	2	3	15
Western Bluebird (<i>Sialia mexicana</i>)	8	12	7
Mountain Chickadee (<i>Parus gambeli</i>)	0	9	7
Western Flycatcher (<i>Empidonax difficilis</i>)	0	5	6
House Wren (<i>Troglodytes aedon</i>)	0	2	1
Total Species	3	7	7
Total Breeding Pairs	19	43	55
Percent of All Breeding Species	18.75	33.33	35
Percent of All Breeding Pairs	21	26	38
H'	1.38	2.56	2.60

were measured he presents convincing evidence that a positive correlation exists between density and the openness of the mid-layer of the canopy.

Root (1967) has probably provided the most complete study available on the habitat requirements of the Blue-gray Gnatcatcher (*Polioptila caerulea*) in portions of California and Arizona. Detailed observations and quantitative techniques stressing the bird, its foraging beat and food were made, and more descriptive techniques used on the habitat. From this it is possible to determine important features of the plant community that are being selected by the gnatcatchers.

Managers should be aware of two considerations brought up by these three studies. Autecological studies can be most valuable in predicting habitat preferences and requisites only in one geographic area and only for the

species concentrated on in the study. For example, the Western Flycatcher, closely related to the Least Flycatcher, selects habitats that are relatively moist, shady and contain a dense understory. The Blue-gray Gnatcatcher inhabits a number of different habitat types throughout its range including woodland, chaparral, forested river bottoms, upland pine woods and broadleaf deciduous forests.

HABITAT ORDINATION

In areas where vegetative communities gradually grade into one another one can look for specific features of the vegetative habitat that may show strong correlations with bird species between habitat types. The vegetational continuum concept (Gleason 1926) and its techniques offers avian ecologists opportunities to investigate bird species diversity

and density along a gradient of continuously varying phenomena. Such studies have been conducted by Bond (1957) and Beals (1960).

By determining importance values and a continuum index based on the relative shade tolerance of the tree species it is possible to arrange plant communities along a numerical scale from most xeric to most mesic and then relate this to the presence and abundance of the bird species (Bond 1957). The results obtained from this work allow one to rank a species by density along the vegetative gradient and then attempt to explain this ranking in terms of the habitat variables.

This approach has been modified and used by James (1970) who measured 15 vegetational variables including percent ground cover, shrub and tree density, canopy cover and tree height at sites determined by the actual location of the singing birds during the breeding season. This allowed her to view specific habitat variables and their relationships among a large number of species occurring over a wide geographic area. The experimental unit is the species of bird and the random variables the vegetation that each species requires as indicated by its presence. James used principal component and discriminant function analysis to order the data set. The first four principal components accounted for 90 percent of the variation. The first component accounted for about 65 percent of the variance, and had high correlations with tree species diversity, percent canopy cover, number of small trees and canopy height. All 15 vegetational variables proved of value in separating species, but canopy height and percent canopy cover were most discriminating.

Recently, Anderson and Shugart (1974) attempted to relate 28 habitat variables, of which 25 were vegetational characters, to 28 species of breeding birds in four plots in an eastern deciduous forest using univariate and multivariate analysis. Each bird was judged as being either present, absent, or having a density greater than one. Univariate, one-way analysis of variance reveals that only four bird species were not significantly associated with any of the 28 variables, whereas five species were associated with 14 or more vegetational variables. As the authors point out, however, the variables are confounded and the results must be interpreted with caution. The use of discriminant function analysis eliminates this confounding and

selects the best single linear combination of all variables. Using this technique on 13 common species that were represented in all three densities, in some cases they were able to determine with a high degree of reliability important vegetational characteristics used by some species. For example, Downy Woodpeckers (Dendrocopos pubescens) had a very high correlation between the discriminant function and the number of sapling trees on the plot. The Carolina Chickadee (Parus carolinensis) was strongly associated with the average size of the understory. By using a three-dimensional principle component space the authors displayed the mean habitat vectors of the 28 bird species, thus showing their similarities and differences for the principle components and each other.

There is no doubt this approach can prove fruitful in developing meaningful variables that can be used in managing habitats for nongame bird species, but thorough testing of this approach will take time and must be wisely planned to insure that the correct set of variables is measured so that the principle components accurately reflect the combinations of factors actually responsible for a bird's presence in the area.

A CASE STUDY

The ponderosa pine forest is structurally a very simple plant community because it is a monoculture and its tree foliage is located in relatively distinct horizontal strata. During the breeding seasons of 1973 and 1974 breeding bird populations were censused (after Kendeigh 1944) on adjacent plots in the ponderosa pine forest near Flagstaff, Arizona, that had been subjected to various timber harvesting techniques. On one plot (17) the foliage volume was reduced to one-third the usual, uniformly over the plot. On a second (14) the foliage volume was reduced to two-thirds the original by clear cutting zig-zag strips through the area and also reducing the foliage volume and tree density in the leave areas, thus creating a large area and number of edges. A third plot (13) was left uncut to serve as a control (Szaro and Balda, unpublished data). One plot (12) was clear cut and others censused only one year. In 1973 breeding birds were censused after a relatively severe winter and very late spring. The 1974 censuses followed a mild winter and relatively early spring. On all three areas there was an increase in

species number, community density and BSD between 1973 and 1974. A number of vegetation measures were computed (after Balda 1969) and compared to BSD.

For both years when BSD was compared to FHD there was a negative correlation or no correlation evident (fig. 7). Within this monoculture, an increase in FHD may have a depressing effect on BSD. Karr and Roth (1971) and Willson (1974) have also shown this and believe foliage gleaners and insect hawkers may have difficulty maneuvering in dense foliage. No correlation exists between PSD and BSD (fig. 7). In this coniferous forest, neither FHD or PSD apparently serve as good predictors of BSD. Figure 7 indicates the probable influence of winter and early spring climate in the BSD. In 1973, when BSD was generally depressed, no correlation existed between BSD and actual foliage volume diversity (FVD), but at higher densities and diversities in 1974 a positive correlation between the two existed (fig. 8). No correla-

tion was observed between BSD and absolute foliage volume (FV) per acre for either year. Of the four measures of foliage configuration (FHD, PSD, FVD, FV) over a two year period only one of eight possibilities showed a positive correlation (FVD and BSD for 1974). We believe our chances of getting a positive correlation for these measures in 1973 were reduced significantly by the depressed state of all populations which we attribute to the harsh, long winter and spring.

In order to ascertain if this pattern was uniformly demonstrated by all species of similar foraging patterns we divided the breeding species into five foraging guilds (i. e. pickers and gleaners, ground feeders, peckers, hammerers and tearers of foliage and/or bark, hawkers and hoverers, and aerial feeders). Foraging guilds show no clear relationship with FHD, except for ground feeders which decline as FHD increases. This group probably relies least on foliage configuration of any of the five guilds. For

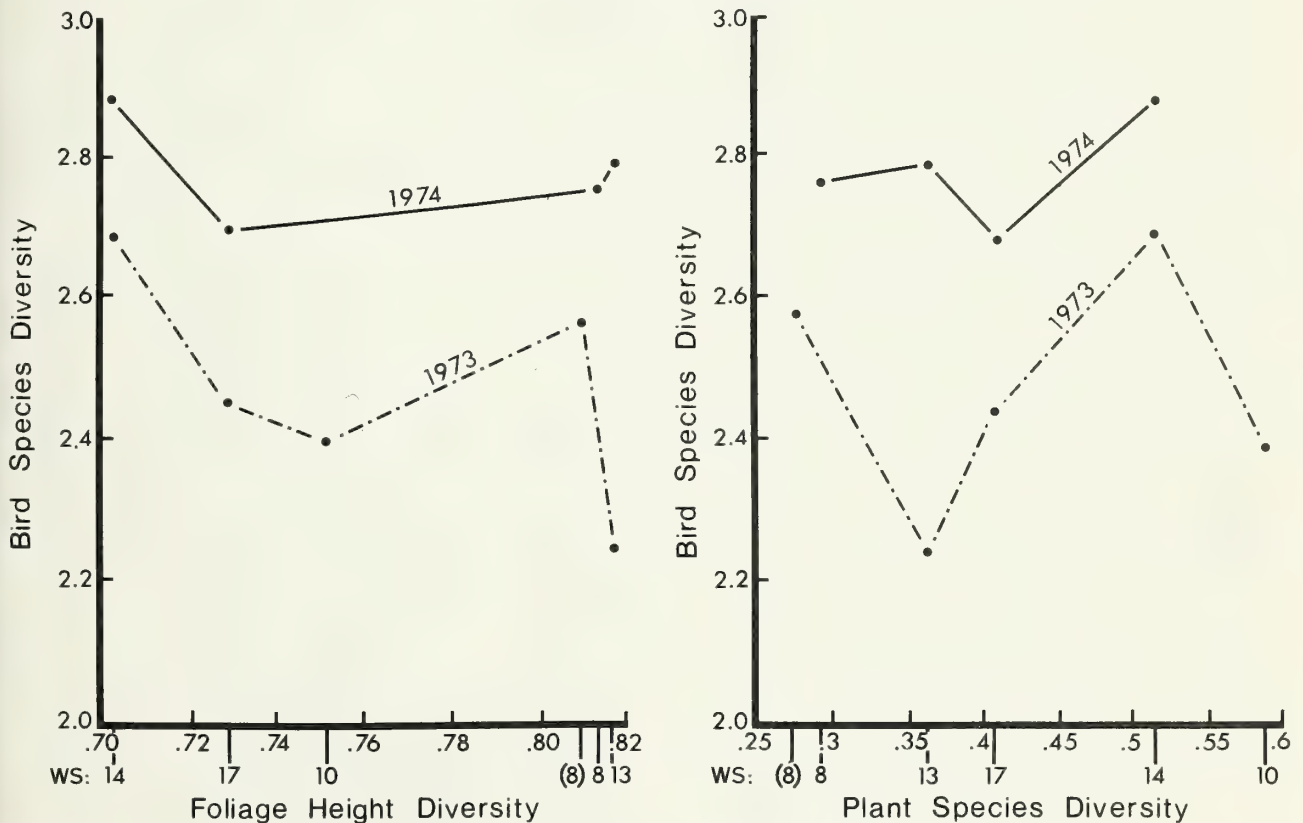


Figure 7. --Bird species diversity compared to foliage height diversity and plant species diversity on ponderosa pine forests cut to different foliage volumes on the Beaver Creek Watershed, Arizona.

FVD, PSD, and FV, no correlation with BSD was evident for either year.

We conclude that factors other than foliage configuration are of overriding importance in determining BSD. This is not surprising, as the ponderosa pine forest is very homogeneous in plant species composition and in physiognomy. Needle bundles, twig configuration, bark pattern, and branch pattern are very similar from top to bottom of the foliage. Inter- and intra-specific relationships may be of prime importance in this situation and require further investigation.

In order to define birds that appeared to respond to changes in foliage density we divided up the species into three categories: birds that occurred on all plots, birds that entered the areas as foliage volume increased and birds that dropped out as foliage volume increased. Within these three categories we then looked for specific trends (increase or decrease in density) with increases in foliage

volume, for the two years of the study (Tables 6 and 7). For species that occur over all foliage volumes the two woodpeckers show no increase in density as foliage volume increases. The foliage gleaning Grace's Warbler increases to a peak and then declines as do the Gray-headed Junco and Solitary Vireo. As foliage volumes increase in density the Robin and Rock Wren dropout but show no trends before doing so. Of the six species that enter the ponderosa pine forest as foliage volume increases four species show a progressive increase in density with increased foliage volume. The density of Steller's Jays does not change once it enters the community whereas the Red-faced Warbler shows no trend.

These trends were most obvious in 1974 when bird densities were relatively high but not so clear for 1973 when bird densities were low. As crude as these figures may be they do give us some initial predictive insights

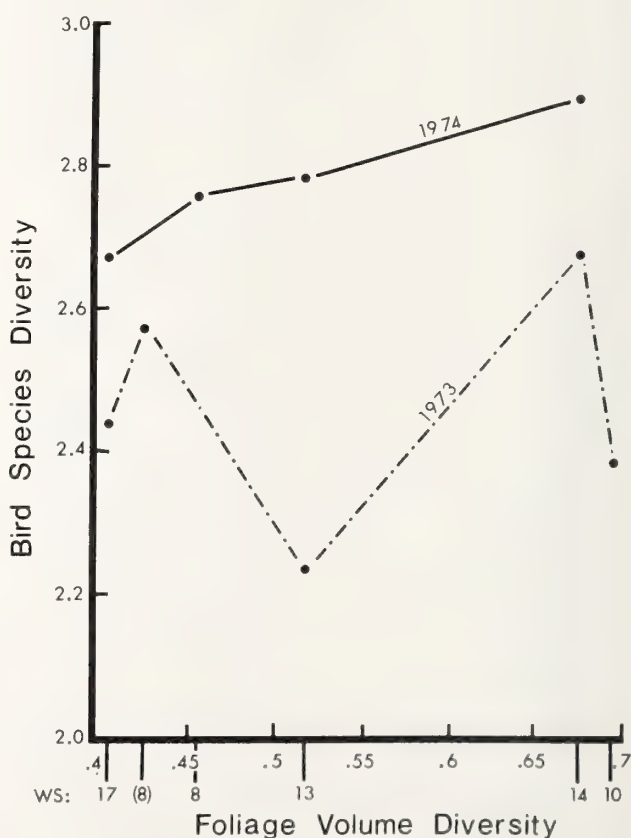
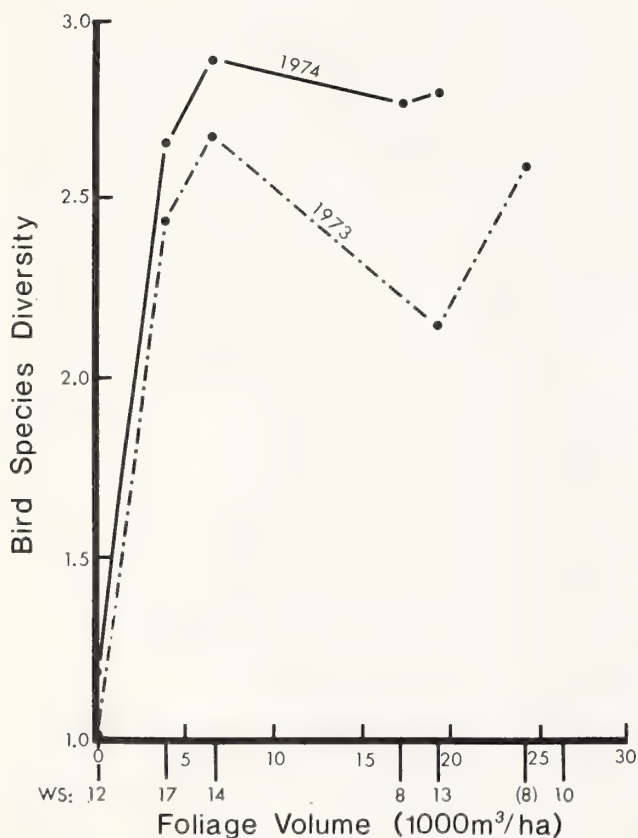


Figure 8. --Relationship of bird species diversity to foliage volume and foliage volume diversity on ponderosa pine forests cut to different foliage volumes on the Beaver Creek Watershed, Arizona.

Table 6. --Birds That Occur on Watersheds that Contain Different Pine Foliage Volumes

Bird Species	1973	1974
Red-shafted Flicker (<u>Colaptes auratus</u>)	= ¹	=
Hairy Woodpecker (<u>Dendrocopos villosus</u>)	=	=
White-breasted Nuthatch (<u>Sitta carolinensis</u>)	-	NT
Grace's Warbler (<u>Dendroica graciae</u>)	+	±
Gray-headed Junco (<u>Junco caniceps</u>)	+	±
Broad-tailed Hummingbird (<u>Selasphorus platycercus</u>)		NT
Solitary Vireo (<u>Vireo solitarius</u>)	NT	±
Western Bluebird (<u>Sialia mexicana</u>)	NT	NT

- ¹ Symbols: = No change in density with increase in foliage volume.
 - Decrease in density with increase in foliage volume.
 + Increase in density with increase in foliage volume.
 NT Variable, but no trend seen.
 ± Increase to a point and then decrease.

Table 7. --Birds that are Absent at High Foliage Volumes and Birds that Enter the Forest with Increased Foliage Volume

Birds That Drop Out With Increasing Foliage Volume

Bird Species	1973	1974
Robin (<u>Turdus migratorius</u>)	- ¹	NT
Rock Wren (<u>Salpinctes obsoletus</u>)	-	NT

Birds That Enter With Increasing Foliage Volume

Bird Species	1973	1974
Violet-green Swallow (<u>Tachycineta thalassina</u>)	-	+
Pygmy Nuthatch (<u>Sitta pygmaea</u>)	-	+
Red-faced Warbler (<u>Cardellina rubrifrons</u>)	NT	NT
Steller's Jay (<u>Cyanocitta stelleri</u>)	=	=
Western Flycatcher (<u>Empidonax difficilis</u>)	-	+
Black-headed Grosbeak (<u>Pheucticus melanocephalus</u>)		+

- ¹ Symbols as on Table 6.

into what happens after timber harvest. It is important to keep in mind that foliage volume may be of some use in predicting changes in bird densities and diversities, it may well be a proximate factor for some species and an ultimate factor for others. The direct relationship between foliage volume and food provided by this foliage remains to be investigated.

DISCUSSION AND CONCLUSIONS

As habitats are modified by natural forces such as succession, fire (Lack 1933, Bock and Lynch 1973) or mans activities (Haapanen 1965, Szaro and Balda unpublished) the avian community will change. There is little doubt that these changes are caused in part by alteration of the vegetation. Some factors are obvious, but often we are unsure exactly what change in the vegetation caused what change in the bird community. In cases where major alterations occur, such as clear cutting a section of forest, the vegetative changes simply cause the removal of all tree dwelling birds, an obvious result. In these cases, the managers major efforts should be to insure that some climax types are maintained. In select cutting, however, modification is more subtle and a portion of the original habitat remains available for bird occupancy. In these cases the managers must be concerned with the requisites provided by that portion of the habitat that has been removed or reduced. Some of these requirements may be ultimate factors necessary for the survival and reproduction whereas others may be proximate factors that contain psychological or "Gestalt" type information. Studies are needed that will relate specific species or groups of species to specific physiognomic features of the habitat.

A number of approaches, at different levels of resolution and from different points-of-view have been utilized by avian ecologists to answer questions about the organization of avian communities and habitat selection by specific species of birds. In some respects, all are useful, and will provide managers with important information, but no one technique will provide all the answers. The obvious reason being the types of questions asked will not generate the kinds of generalities needed by land managers to define the constraints imposed by different habitat alterations.

I urge land managers to be cautious in using data gathered over only one season or from a short period of time during one season. As was pointed out earlier, fluctuations in densities and numbers of species as well as general population trends based on foliage characteristics may be totally obliterated by climatic conditions. A recent situation I was confronted with may help make this point. If we are concerned with how many snags to leave in a pine forest for secondary cavity nesting species, we need to know the number of pairs of secondary cavity nesters inhabiting areas with a natural component of snags and the approximate proportion of those pairs that will nest in holes in live trees. If census information from a year when densities are low is used, the calculated number of snags necessary to support the population will be greatly underestimated, but thereafter the population will not be able to recover to optimum levels because nest sites are lacking. One can argue that the situation can be easily rectified by simply putting up nest boxes. Our studies have shown that about 70 percent of the winter resident birds are cavity roosters as well, thus the boxes may need to be insulated and maintained for winter roosts as well as for nesting. Brown Creepers (*Certhia familiaris*) nest under exfoliating bark on snags and not in holes; thus, we will still possibly lose a potentially valuable insectivorous species of the Western Coniferous forest. In addition, I know of no study in this country that attempts to give snags their due consideration when characteristics of the vegetation are measured and compared to some characteristic of the avian community. Besides providing nest and roost sites these snags also serve as caching sites for some species of woodpeckers.

The most common variables of the vegetation measured in most studies reported on herein include foliage volume, tree height, foliage height diversity, etc. In some cases these measures are not adequate to define the resource being used by the birds. Most studies reported on herein (Austin 1970, Anderson and Shugart 1974, Balda 1969) simply use the entire plant community as the independent variables. In many cases, actual bird use of these variables has not been measured and the workers have relied strictly on correlational measures to link bird species diversity to some characteristic (s) of the vegetation. Anderson and Shugart (1974) did use small plots and James (1971) measured

areas that had a specific species present but most studies do not. Balda (1969) linked specific use of the foliage by birds to the amount of foliage available. Wiens (1969) and Sturman (1968) measured habitat variables in areas that were defined by the birds. The latter authors statistical approach as well as that used by James (1971) and Anderson and Shugart (1974) deserves careful attention but additional information including bird use should become part of the analysis. It is then necessary to attempt to match principal components derived from the habitat measures to those derived from measures on specific species within the community. Such a study is now underway for the ponderosa pine forest.

There is no panacea to be found in what has been done to date to answer the questions asked by land managers. Often, generalities have come from very specific geographic areas or where only a minimum of habitats have been investigated. In some cases, investigators have used a priori reasoning and varied the number of foliage height classes or the cut off points determining height class in order to obtain a best fit between such parameters as foliage height diversity and bird species diversity. In many cases, if one tries enough permutations of the raw data, a correlation can be found. Often then some scientists have felt that because it works, use it, even if the biological explanation for its use is tedious.

It has been said that a successful criterion for managing nongame birds is diversity. Thus one could envision successful management as removing all climax vegetation types and setting them back to some earlier successional stage, if that stage has a higher diversity than the climax. This view may seem extreme but would achieve the desired results. In this process, one could also eliminate the presence of one rare, valuable species high on the food chain. The removal of a traditional nesting tree of a Goshawk (Accipiter gentilis) is a good example of this. Rare species are given little weight in diversity measures such as H' yet these very species may be intrinsically valuable to the maintenance of the community. Another example of this impersonal approach would be the replacement of Eastern Bluebirds by Sialia sialis by Starlings (Sturnus vulgaris).

The alternative I offer is to manage a forest to maintain the maximum number of species at density levels that most closely

reflect natural conditions. A well-managed grassland at the base of the Chiricahua Mountains, Arizona supports 4 species of breeding birds whereas a highly overgrazed grassland that has been invaded by shrubs and succulents supports 20 species (Balda 1967). It is difficult to conceive of this practice as achieving a management goal. I maintain a natural grassland will be most productive and beneficial to mans needs if managed in such a manner as to maintain the natural components of the system. These components do not occur together in some random manner but have succeeded through time together because some optimum level of efficiency has been achieved through the process of natural selection.

Although vagrant edges and permanent ecotones (transition zones) are usually assumed to have higher bird species diversity than the communities that flank the ecotone, there is little support for these ideas from these ecotones in some areas of the mountainous West. Thus, I urge caution in accepting this broad principle. Creating small edges by opening forest characterized by dense foliage will most likely attract additional species. I should think a goal of management would be to maintain species composition and density rather than modify it. Many species of birds attracted to edges have rather broad ranges of tolerance, good powers of dispersal and high reproductive rates (one could refer to some of them as "weed species") and are in no immediate danger because of habitat destruction and deterioration. It is species with very narrow ranges of tolerance and possibly minimal powers of dispersal that need our attention, and seldom are these edge species. As Haapanen (1965) points out, "It is much more difficult for the species of climax stage to adapt themselves to a cultivated environment."

In conclusion, I would like to stress the following points:

1. Bird species appear to select their habitat based on a constellation of factors including life-form of the vegetation (Pitelka 1941) which may be both an ultimate and/or proximate stimulus as well as the presence or absence of certain vegetative strata (MacArthur and MacArthur 1961, MacArthur 1964, Karr and Roth 1971) and the height of the vegetation (Lack 1933, Cody 1969, Wiens 1969). One wonders if the height of the vegetation might not reflect the amount of foliage

that is synthesizing most rapidly. These areas also produce young tender shoots, needles, leaves, buds, and cones which may be attractive to birds or to insects that are eaten by birds.

2. Much of the work done to date on bird species and their habitat components is solely correlational in nature and in the conclusions drawn from it. It is time for more critical studies that actually link birds to their habitats. Multivariate analysis and multiple regression techniques may offer the best insights to the problem. At present, we have no simple technique or generalities to predict species diversity from habitat variables that can be applied on a nation-wide basis. Hopefully a result of this symposium will be an attempt to develop such a list in a form usable to managers.

3. A more careful assessment of the requirements of the birds needs to be made as they relate to such factors as correct insect food, nest and roost sites and nuts and berries. Much of this information is in the literature and simply needs compiling and put in a form usable by managers.

4. Managing solely for species diversity may be a mistake as the approach is far too impersonal from the birds standpoint and can allow valuable but rare species to be completely removed from the habitat. Just as we manage game birds on a species specific basis we need to approach nongame bird management from the same point-of-view.

5. Until we have the necessary information on specific habitat types on a regional basis a goal of land managers should be to maintain as many naturally occurring habitats (especially climax communities) as possible, as a little knowledge may be more harmful than good. This will allow future generations the same options we have today.

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Habitat Management Implications of Migration¹

Alexander Sprunt, IV^{2/}

Abstract.--Birds utilize most available habitats during their migrations. Some habitat types are more important than others while the location of still others makes them vital. Diversity is a key to good migrant habitat and should be considered in management planning.

INTRODUCTION

When I accepted the invitation to take part in this Symposium and to speak on my indicated subject, I'm afraid that I did so without giving it a great deal of deep thought. In the months that have passed I have tried to find sources of information that would help in the preparation of the paper and have come up notably wanting.

The migration of birds is a natural phenomenon that has fascinated men since ancient time. Authors of the Bible, Homer, Aristotle, Pliny and others through the years have commented on the fact of migration and attempted to explain it. If this paper had been prepared in the Greece of Aristotle we would have been advocating the creation of "retreats" where swallows and turtle doves could go to drop their feathers and spend the winters in a state of torpor, or if we followed the advice and belief of Olaus Magnus, writing in 1555, we would provide lakes and marshes where swallows could dive beneath the water and remain jammed together in a large ball through the winter!

A great and happily more accurate literature covering migration has been amassed in the time since the above, most of it since the 1850s. There are now literally thousands of titles dealing with the causes of migration, its origins, timing, routes followed, the effects of weather, the physiological aspects, and more recently, the fascinating subject of bird navigation and orientation but in not one title or in a single paper is the question of habitat or habitat management treated directly! So, the material presented here must be looked at in this light. Most of it is deduction and to a degree subjective, based on my own experience and the experience of those with whom I have discussed the problem. It will of necessity be rather general in treatment. I am sure that there may be shortcomings and perhaps large gaps in the material to follow. I hope that my colleagues will be willing to add to my thoughts during the discussion period to follow.

MIGRATION

The term "migration" has been variously interpreted by different authors. It behooves us, then, to begin by defining migration as it will be used in the present discussion. I prefer the definition used by Dr. Jean Dorst in his book, "The Migration of Birds." I quote, "Migration...a series of periodic 'round trips' - usually annual - in the course of an animal's life cycle between a breeding area - called 'home' - and a region where the animal spends a period of varying length outside the reproductive area and which it then leaves to go back to its 'home'."

Migrations are common throughout the animal kingdom but they are most conspicuous among birds which have well developed specializations for long, swift travels. Birds are also extremely dependent on the habitats in which they find themselves. Their high rate of metabolism necessitates a rich source of food, which may be only seasonally available in one region, while their egg laying mode of reproduction causes special problems of proper environment for the eggs and young. These factors help explain why birds perform the most marked and

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best defined migratory movements.

Among birds there are several different types of migration. The classic type is best developed in the colder parts of the northern hemisphere where severe winter conditions force many birds to move long distances to find congenial winter quarters. The migrants that move over the greatest distances are those that breed in such places.

Shorter movements which may be altitudinal or lateral accomplish the same results but may be caused by seasonal food availability or other factors.

Within species migratory movement may vary, with members of the same species showing different modes or lengths of migration in response to different conditions. Thus, fox sparrows on the Pacific coast show highly developed, long distance movement in northern populations, while more southern populations move to a lesser extent or not at all. In fact, it has been shown (Swarth 1920) that the more northern form winters farthest south, "leap frogging" over more sedentary forms.

Birds differ not only in the magnitude of their movements but in the time of day at which movement takes place. There seems to be a definite tendency for particular species to be either diurnal or nocturnal in their migrations. Most small birds, including rails, flycatchers, vireos, wrens, warblers and tanagers, are nocturnal migrants. Large, strong-flying birds tend to be diurnal in their movement. These include loons, cranes, gulls, pelicans, hawks, swallows, nighthawks and swifts (Lincoln 1939). The preference shown for day or night travel is probably primarily a result of the need for adequate food during the migration period. Small birds which make their long flights at night are thus able to spend their days in alternate feeding and resting, refueling as it were, for the next move. Diurnal migrants on the other hand are species which can feed on the wing, such as swallows and nighthawks, or are birds which utilize thermals and other wind currents for soaring flight, such as pelicans or raptors, or water birds that follow coasts, etc.

There are other differences in the diurnal and nocturnal migrants. Nocturnal migrants tend to move on broad fronts with thousands of birds moving over long distances in a night. Diurnal migrants are much more likely to follow topographic features such as river valleys, mountain ridges or coastlines and tend to move in more restricted lanes or pathways.

In North America many of the major land forms lend themselves to use by migrants due to

their north-south orientation. Both coasts, the Appalachian ridges, Mississippi Valley, Rocky Mountain chain, the Sierra Nevada and Cascade ranges all are major routes used by migrants.

Certain land forms and/or habitats can have strong attraction for migrants while others can repel them. Both reactions can have an effect on migration routes. Many migrants follow valleys, for instance, but show reluctance to cross wide expanses of open water or even refuse to do so. Such attraction and avoidance reaction can have a concentrating effect on migration routes and result in the buildup of numbers of migrants to impressive proportions in certain areas. Such spots include the western end of Lake Superior, Pt. Pelee, Ontario, Cape May, N.J. and Cape Charles, Va.

Migratory movement takes place over most of North America but information gained through banding has shown (Lincoln 1935) that there are four more or less distinct pathways followed by the majority of birds. This is best documented for waterfowl but the concept is generally applicable to other groups. These pathways, or "flyways" as they have been called, are: the Atlantic, Mississippi, Central (over the great plains) and the Pacific. Certain shorebirds follow, at least in fall, two additional flyways, one over the Atlantic Ocean and the other over the Pacific.

HABITATS UTILIZED

Birds are highly mobile creatures. They are also quite adaptable as a group and have shown a high degree of capability in utilizing varied habitats in the course of their migratory movement. Indeed, it can probably be said that every habitat present in North America is used by some bird in the course of its migrations.

Because of the great mobility of migrants, the effect of habitat destruction may not be readily or immediately apparent. The effect of the destruction of a given block of forest, for instance, can be overlooked easily due to the birds ability to go elsewhere. A species that moves several tens or even hundreds of miles in a night can easily move a few miles right or left, stop short or, in some cases, go farther to reach suitable habitat. The cumulative effect of habitat removal, then, can be subtle and take a long time to assess.

Some types are obviously more attractive to a greater number of bird species than others and a review of some of these follow. The habitat needs of migrants are similar to birds everywhere, that is food, water, and shelter.

Forest Types

Deciduous and coniferous forests are utilized by a great many birds for their major food supply, not only during migration but during the rest of the year as well. The diversity of ecological niches which are available and the tremendous diversity of life found in them form one of the major biotopes of the continent and are thus of major importance. These can be further broken down, however.

As stated earlier it is well documented that mountain ridges form an important aspect of many migrant's world. The still existing forests on many mountains form lanes through areas that have been transformed into open types through agriculture or grazing and thus form natural pathways for species dependent on forest.

Another function performed by ridges is the creation of strong and persistent updrafts under certain wind conditions. This leads to the use of certain corridors by soaring migrants annually. Hawk Mt. in Pennsylvania is probably the best known but certainly not the only such feature (Broun 1948).

Another forest type that can be of extreme importance to migrants is riparian woodlands. As previously mentioned, river valleys are frequently used as major migration routes. The Mississippi Valley probably carries more and a greater variety of migrants than any other comparable land area on the continent. Riparian and flood plain forests are producers of food for a myriad of nocturnal migrants but are also important to diurnal travelers. Flycatchers, swallows and others follow the forest located on and adjacent to the Mississippi and Missouri levees in large numbers.

In areas of the arid and semi-arid West, where many rivers are oriented across the path of most migrants, the strips of riparian woodland can be vital to migrating passerines. They constitute havens of refuge and food sources to break the journey across unfavorable terrain and allow many forest species to successfully cross grassland and deserts. The present trend in many areas to destroy riverine forests in the name of saving water or "phreato-phyte control" is certainly as harmful to migrants as it is to resident breeding species.

Forests located in several of the concentration points mentioned earlier can be important far beyond their size. The protection of strategic areas such as Wisconsin Point at the west end of Lake Superior, patches of woodland at Cape May, N.J., or Cape Charles, Va. would be highly beneficial to migrants of many species. The destruction of native forests in the Florida

Keys, which is going on presently, is an example of this sort of adverse impact.

Closely allied to the preceding types are landfall areas. One of the most striking aspects of North American bird migration is the movement of many passerines over the Gulf of Mexico. In good weather with light or southerly winds migrants from Yucatan may cross the Gulf coast and move far inland, perhaps as far as Tennessee (Lowery 1945), before coming to earth. This phenomenon has been called the coastal hiatus. When trans-Gulf migrants meet headwinds or stormy conditions, however, literally tens of thousands of birds may be precipitated on the northern Gulf coast in a single night. The narrow oak ridges of the Louisiana coast, called "cheniers," and wooded coastal islands are of utmost importance to these birds, providing a place to rest, feed and find suitable cover before moving north again. Areas of this woodland type should be preserved.

Islands and island chains can also be of great importance to migratory birds. The almost continuous chain of islands around the eastern side of the Caribbean form a pathway used by a number of species moving between North and South America. Smaller islands which are located within heavily used migration routes can also be important. One island of this type is Block Island, R.I. During the fall birds moving down the Atlantic coast at night might be drifted offshore by west and northwest winds. Many of these birds collect at daybreak and hundreds or thousands may make a landfall at Block Island. Wooded areas there serve the same function as described for coastal islands along the Gulf.

The Dry Tortugas, 70 miles west of Key West, lie in the path of some trans-Gulf migration and are also used as stopover points by migrating passerines. One type of habitat management has been quite successful there, the provision of fresh water to the migrants. The islands have no natural fresh water but it has been artificially provided by the National Park Service and the Tropical Audubon Society in the shape of bird baths and drinking fountains and is eagerly utilized.

Islands such as these are of aid to many migrants of diverse types. On both Block Island and the Tortugas raptors have taken advantage of the easy targets represented by tired migrants and peregrine falcons and other species can be seen taking toll of the smaller birds.

Range Types

Many types of range land are equally as important to migrants as forested types. Many

of our shorebirds and grassland species move over the prairies and through the Great Basin provinces. These make extensive use of natural grasslands. One of the more important aspects to migrants of the prairie areas are the wetlands, both natural and man-made. The importance of prairie wetlands to waterfowl is generally recognized but many more migrants are just as dependent on them. Sandpipers, avocets, curlews, plovers, phalaropes, rails, blackbirds, gulls, and many other species utilize these wetlands. A trip to a prairie pond or marsh in spring or fall is a rare treat to a bird watcher.

The present widespread channelization of streams and drainage of prairie ponds and pot-holes can affect migrants as well our stocks of waterfowl.

The importance of grasslands to certain migrants is best documented in the case of shorebirds. Golden plovers utilize them extensively in spring migration as do buff-breasted sandpipers. The conversion of much of the southern, coastal prairie in Texas from grazing land to agriculture could have been one of the factors leading to the demise of the Eskimo curlew (Palmer 1967).

Interspersed with the grasslands are other vegetation types; brushlands, thickets, patches of weeds are all found in stream bottoms and low places. Harris' sparrow seems to be almost confined to these types and utilizes them during migration as well as for wintering.

The shelter belts that were advocated during the 1930s throughout much of the western rangeland have definitely had an effect on the distribution of migrants as well as breeding populations of birds. The presence of trees in areas where none existed previously has allowed eastern, forest-oriented species to move westward. Migrants move from shelter belt to shelter belt and now are commonly seen in areas where they were once rare or non-existent.

Special Types

A number of habitats are of greater importance to migrants than is readily indicated by their size or acreage. Wetlands are certainly one of these. Fresh and salt water ponds, lakes and marshes are used by a great many species and individual birds. The protection of existing wetlands and the creation of new ones have a potentially profound effect on migration.

In the recent history of wildlife management in North America the widespread creation of refuge areas, most of them wetlands, has changed the migration patterns of a number of

species of waterfowl. The short stopping of Canada geese and other geese that used to winter on the Gulf coast is a well known phenomenon. Refuges farther north, by providing wetlands and food, have caused the birds to remain north of their ancestral wintering grounds. While the alteration of the migratory pattern is better documented for the waterfowl, it has almost certainly affected nongame species as well. Our own work has shown a redistribution of certain heron colonies.

Water is a powerful attractant for many migrants. Agricultural lands that are partially flooded to provide shallow water or muddy flats are particularly attractive to shorebirds and the provision of such areas during the migration period can result in spectacular concentrations.

Coastal areas are utilized by many species during migration. Shorebirds, some inshore seabirds, and many passerines follow beaches, back beaches and shallow inshore areas and use the same regions as feeding and nest sites. The prevalence of raptors, particularly peregrines, on beaches is recognized and counts made on beaches are used as an index of the population. There is an ever increasing pressure for human use of our beaches. The importance of this habitat type to migrants should be a management consideration.

Some migrating birds use traditional flight lines for many generations. For some species there are points along these pathways that supply essential needs at specific times. These points usually become staging areas where the birds concentrate and stay for a time before continuing. Examples of such areas are several. Adult golden plovers from the eastern Arctic of North America gather in fall in Labrador, Newfoundland and Nova Scotia where they feed before taking off for their flight to the northern coast of South America. Sandhill cranes from much of the central U.S. and northern Mexico gather in huge numbers along a stretch of the Platte River in Nebraska each spring on their way north. This area is now threatened by a Bureau of Reclamation project which would de-water much of the river. The project would eliminate the shallow gravel bars used by the birds for roosting and could make the area untenable. There are now more birds on the Platte than there were 20 years ago. This could be due to the restriction of available habitat elsewhere. The loss of the Platte could prove disastrous to the population (Madson 1974).

Some species have altered their wintering areas in response to man-made changes in the environment. One striking example of this is the winter distribution of bald eagles in the Missouri and Mississippi Valleys. Eagles have

always been found along the major river systems of the continent. The building of large reservoirs has, however, created sources of more readily available food for bald eagles and has led to concentrations of our national bird at locks and dams. The turbulence and temperature changes created by the dams and reservoirs keep these sections of the rivers open, and power plants and spillways provide a supply of injured fish. Migrating eagles now stop off to take advantage of the easy pickings. In some areas roosting sites for these eagles are important and several of them are now being acquired and protected for the use of the birds.

Sites such as those mentioned above should continue to be identified and preserved where necessary.

Problems Caused to Birds

Man, in his wholesale alteration of habitats, has caused a number of problems to migrating birds. The flexibility and mobility of the birds themselves have minimized these effects but they have nevertheless had an impact. The general reduction of many habitats, such as forest in the east and natural grasslands over much of the mid-west, has certainly stressed many birds, particularly inexperienced young birds during their first migration. This is impossible to measure but undoubtedly has some effect.

Another habitat alteration is the erections of obstacles by man within the path of migrating birds. The direct toll of migrants caused by many types of obstructions is well known. Lighthouses, bridges, T.V. towers, buildings and celometers have all been known to kill thousands of birds. In some cases the loss of life takes place only under certain weather conditions but at a few sites birds are killed on a regular basis throughout the migration period. The building of particularly damaging structures such as tall T.V. towers and other antennae with their maze of guy wires should be avoided in heavily used migration pathways.

Problems caused by Birds

Another aspect of habitat management is that which leads to problems of man, caused by birds. In many cases such problems are directly caused by man's own alteration of the habitat. The recent difficulty with blackbirds at Fort Campbell, Ky. is a good case in point. This roost of wintering blackbirds, which posed a threat to human life through hazard to aircraft and to public health, occurred at a planted pine plantation. These close-spaced pines provide an ideal roosting site for these colonial

species of blackbirds. The reaction in this case was to control the birds but the problems could have been resolved, and we hope will be resolved in the future by the thinning or destruction of the created habitat.

The concentration of birds around airports is often a function of mistakes in habitat management. In many cases the birds have not been attracted to the airports but the airports have been taken to the birds. The creation of airports on active sanitary land fills where garbage is placed in wetlands, for instance, is guaranteed to produce a gull problem. Proper consideration of birds and their problems during the planning phases would go far toward eliminating such conflict in the future.

Crop depredations are another problem area where migrants and humans often conflict. Grain damage by cranes at their staging area at Last Mountain Lake in Saskatchewan, for instance, could be reduced or alleviated by a change in harvesting practice or in the retirement of some fields where cranes congregate. Depredation on corn in western Ohio is a direct result of planting corn in an area which is located in a concentrated corridor of migrating blackbirds moving down the Michigan Peninsula and adjacent Ontario and funneled into a narrow corridor by the configuration of the lakes. Farmers probably would be better off in the long run to convert to soy beans or at least a variety of corn which is earlier maturing or resistant to blackbird damage.

MANAGEMENT SUGGESTIONS

It is obvious from the discussion so far that bird migration does have a number of varied implications for habitat management. Some specific points have been developed.

1. There has been little consideration of the problems of migrating birds in the development of most land management plans. Habitat managers should become aware of the needs of migrants and be alert to the possibilities of enhancement of habitat for migrants. A specific feature may have much greater effect in some contexts than in others. A row of trees along a prairie stream has much greater value than the same row between two fields in a mixed woodland-pasture region.

2. Certain areas have much greater value to migratory birds than their extent would indicate. Such features as concentration points, landfall sites and staging areas should be looked for, identified and suitable action taken.

3. Managers should be alert to migrating birds during the appropriate time of year and to

look for any specific needs that are not present such as water in arid areas, brush cover in prairies, etc.

4. Diversity is the key to heavy use of most wildlife areas. The opportunity to increase diversity often exists. Create a marsh, flood a fallow field, pump down an impoundment to create mud flats. Such actions during migration periods can aid a variety of species.

To sum up, much more attention could be paid to our migratory birds. Their needs are similar to resident wildlife but special attention to certain aspects of management have the potential of enhancing many habitats for the use of migrants. This in turn has the potential to adding to the diversity and interest of the avifauna of any given area.

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Discussion

MR. THOMAS: I have two questions. First, Dr. Verner, you indicated that the minimum population required to sustain a species was unknown. Similarly, the minimum territory required was unknown. I would like to have you comment further. Mr. Balda, while waiting for the data on several hundred species, and for the ability to manipulate the multiple matrix of treatment, plant community, and expectation stages, what is our input into timber planning?

DR. VERNER: The time required to get data on the minimum number of pairs of birds necessary to maintain population probably wouldn't make that line of research very productive. I recommend that we focus attention on larger species, particularly raptors and larger insectors. Since their territories are so large compared to those of most nongame birds, their protection may insure adequate conservation of other species. We may never find the minimum, the bare minimum of pairs that would maintain a species or the area necessary. We are dealing in terms of evolutionary time. We can't predict catastrophies. We can't foresee such vagaries as introduction of a new species.

MR. BALDA: I recommend some kind of common sense approach, whereby we try to maintain the diversity of natural communities. I don't believe that 800 species must now be considered in management. There are a lot of species that will make it in altered habitats. I am worried more about what we do with our climax forest and those species that nest there. And I am concerned about those species that are present there, not the fact that there's less diversity there.

MR. LENNARTZ: Dr. Balda, you made the statement that managing for optimum or maximum diversity was an easy way. If we take the very limited view of a single stand or single habitat and single point in time, your comment is perhaps correct. But instead of keying in on the stand, we must consider the entire forest. Instead of looking at an instant in time, we consider the entire management rotation. Then management for diversity is a viable concept.

MR. BALDA: The challenge, as I see it, is to manage for natural diversities. For example the Chiricahua grasslands that I studied in 1957 had four species of breeding birds. On the overgrazed land there were 15 species of

breeding birds. I would hardly look at that overgrazed grassland with its cactus and its yucca as management success.

MR. DAVIS: Dr. Balda, what are the impacts of complete removal of overstory on 50 to 1,000 acres of ponderosa pine?

MR. BALDA: The entire bird community is changed. The ponderosa pine birds go when the ponderosa pine trees go. In some areas dense thickets of ponderosa pine occur. Those can all go without affecting bird density or bird species diversity. I know of no species that is restricted to or makes any significant use of thickets.

MR. KINGSLEY: Dr. Peterson, how do interested people become participants in the survey?

DR. PETERSON: Inquire at the Patuxent Research Center. We are seeking greater participation.

MR. WAYNSBURG: You were suggesting, Dr. Peterson, that the roadside community provide a kind of general index for management strategy for nongame species. I simply want to comment that this may be true only when one is operating a broad regional level for resolution. Use of roadside counts as an index for the wellbeing of avifauna character of a given habitat, is a very dangerous procedure.

DR. PETERSON: This is a big problem in roadside counts. Anyone who has analyzed roadside counts will realize there are many biases involved.

DR. JAHN: Any other questions or comments?

MR. JANTZEN: Mr. Sprunt, you expressed concern for migrants. I wonder what can be accomplished in this country without any controls or expertise or any management practices being applied in South America, Mexico and on down.

MR. SPRUNT: You are speaking to the deterioration of wintering habitats all through Mexico and Central and South America, but I don't think that saying that somebody else is causing the problem is any excuse for us not doing what we can on this end. This is of course a very serious problem. We are very fortunate that migratory birds during that period of existence are mobile and can take advantage of existing

habitats that still persist. The problem certainly exists.

MR. WESKE: Friends of mine have found that in Panama North American migrants are less habitat

specific, not going necessarily for undisturbed forest but for secondary habitats. This may mean the situation is not as black as we imagine.

Wednesday Morning, May 7

Management of Deciduous Forest Habitats

*Presiding: W. E. Towell
The American Forestry Association*



Dominant Patterns in Bird Populations of the Eastern Deciduous Forest Biome^{1,2}

H. H. Shugart,³ S. H. Anderson,⁴ and R. H. Strand³

Abstract.--There are several general patterns of variation evident in bird populations of the eastern deciduous forest biome. The avifauna of the eastern forests is typically dominated by migrants and there is a pronounced increase in the bird standing crop during the breeding season. The importance of birds as components of ecosystems stems from their mobility and from their high trophic position on many food webs. During secondary succession, bird populations typically increase in density, diversity, and standing crop with time. The energetics of bird populations in forests are strongly correlated with the densities of the population. Habitat selection is an important determining factor for bird distributions and habitat factors are generally more important than food-availability factors in avian resource division. Discriminant function analysis is demonstrated as a potential research tool for determining bird habitat preferences.

INTRODUCTION

Of the several hundred indigenous bird species within the eastern deciduous forest biome, only a very small percentage are considered game birds. The non-game birds have typically been studied by ornithologists interested in systematics, zoogeography, behavior and other relatively esoteric subjects; whereas game birds have been studied by wildlife scientists interested in yields, productivity and such pragmatic considerations as keeping the local hunt clubs happy. Over the past several years the law, the attitude of the public, and the patterns of outdoor recreation

have created an atmosphere that calls for ornithological research to supplement information and to offer guidelines to the landscape manager as well as a need to synthesize what is known about non-game bird populations. In this manuscript, we will attempt to generalize on the pattern of bird populations in the eastern forests and will identify one research method of potential utility in non-game management research. Our topic is the common patterns of the common birds of the eastern deciduous forests, and we recognize that there are exceptions to the general patterns that are presented herein.

TEMPORAL PATTERNS OF BIRD POPULATIONS

Welty (1964) states that, "Of the species which breed in the deciduous forests of North America, about three-fourths migrate south for the winter." One manifestation of this feature of deciduous forest avifauna is a pronounced increase in bird standing crop during the summer breeding-season. This pattern is in contrast with the less variable seasonal populations expected in coniferous forests (Fig. 1). Our emphasis in the present paper will be the ecological aspects of breeding bird species in

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deciduous forests. This emphasis is in part due to a relative lack of nonbreeding season studies in forests.

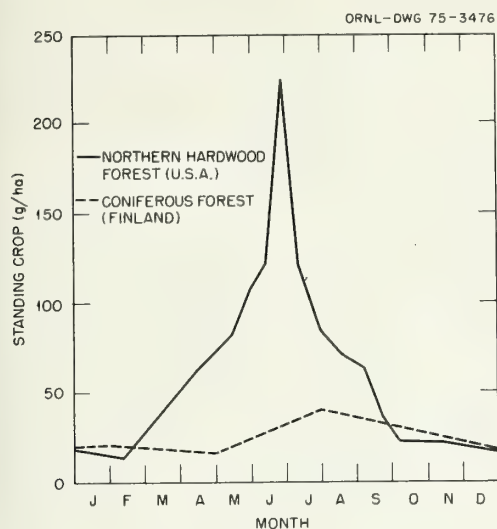


Figure 1.--Seasonal changes in avian standing crop in coniferous and deciduous forests. Data for northern hardwood forest from Sturges et al. (1974) and for coniferous forest from Nuorteva (1971).

THE ECOLOGICAL ROLE OF BIRDS

Although there are numerous anecdotal examples of the importance of birds (or a given bird species) in maintaining the integrity of forest ecosystems, *it is generally difficult to demonstrate unequivocally that a given bird species has any important regulatory role in a forest ecosystem.* There are examples of apparent reduction of beetle outbreaks by woodpeckers, reduction of insect pests by artificially increasing bird density, as well as a number of other proposed important roles of birds, but there is to date little experimental evidence of any dominant ecological role unique to birds. This is probably due to the still embryonic state of our understanding of ecosystem function, and the assessment of actual importance of birds to the forest ecosystem must be delayed until more information is available. However, there are some general features of birds that are important to consider in ecosystem studies:

1. *In a forest, the top carnivores are predominantly birds.* Materials that concentrate up food chains (DDT, heavy metals) tend to reach their highest concentrations in birds. Thus, birds are both the most sensitive ecosystem component and the indicator for the effects of certain toxic materials.

2. Although birds generally account for

a relatively miniscule part of the turnover and standing pools of energy, biomass, and essential elements, *birds occasionally have a significant role in element turnover in forest ecosystems.* For example, Sturges et al. (1974) found that while birds were generally insignificant relative to the energy and material budgets of the Hubbard Brook Watershed (New Hampshire), bird migration accounted for 16% of the net phosphorous loss from the ecosystem.

3. *Birds are generally the most mobile components of an ecosystem.* This feature is often implicated in seed dispersal and in the vectoring of various diseases over broad geographical areas.

BIRD POPULATION PATTERNS DURING SUCCESSION

Patterns of Bird Species Diversity

One standard measurement for the comparison of different communities is the species diversity index, $H' = -\sum p_i \log p_i$, where H' is the value of the index, p_i is the frequency of occurrence of the i th bird species (see MacArthur and MacArthur, 1961; Patten, 1962; Lloyd and Ghelandi, 1964; Monk, 1967 for various applications of this index in different types of organisms). The species diversity index increases with both the richness (the number of species) and the equitability (the evenness of numerical abundance among species) of a given community. Tramer (1969) and Kricher (1972) found that in a great variety of bird communities, the differences in diversity indices were due primarily to the species richness of the communities. Tramer's work in particular implies that *for birds a species diversity index does not contain a great deal more information than a species list.* The diversity index is not as strongly influenced by rare species as is a species list, and thus is useful in comparing studies in which the sampling intensities might differ (Buzas and Gibson, 1969).

The expected pattern of species diversity through succession is one of a general increase with a decline in the last successional stages (Margalef, 1958). Studies on bird populations in deciduous forests have not verified this predicted pattern. Adams (1908) listed characteristic bird species of successional states (aquatic communities to bogs to climax forests) on Isle Royale, Michigan. Adams did not measure species diversity but he noted a greater variety of bird life (richness of species) in the intermediate stages of succession rather than either the climax or the pioneer stage. Figure 2 shows the pattern of species diversity for three more recent studies (Johnson and Odum, 1956; Karr, 1971; Shugart and James, 1973). In no case is a decline in species diversity in late succes-

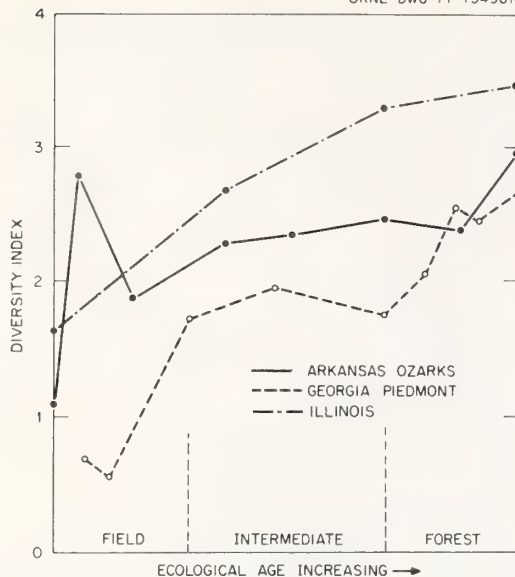


Figure 2.--Changes in the species diversity index (H') for bird communities during ecological succession. The Arkansas data are from Shugart and James (1973); Georgia data from Johnson and Odum (1950); Illinois data from Karr (1971). Figure modified from Shugart and James (1973).

sional communities evident, although there is a general increase in diversity through succession. The Arkansas study has one diverse old-field community that does not appear to be due entirely to sampling variation (Shugart and James, 1973). It is important to note that among the three study areas *there is considerable variation evidenced in the pattern of species diversity of birds during succession.* This variation proscribes the designation of a single "typical" bird diversity pattern with forest succession in the eastern deciduous forest biome.

Patterns of Avian Density

An increase of avian density through a progression of successional communities has been documented by Saunders (1936) in New York, Kendeigh (1948) in Michigan, Odum (1950) in North Carolina, Johnston and Odum (1966) in Georgia, Haapanen (1965) in Finland, Karr (1968) in Illinois, Karr (1971) in Panama, Shugart and James (1973) in Arkansas. These findings drawn from diverse regions are in general agreement. There are notable exceptions to this general pattern [e.g., Kendeigh (1947) found highest bird densities in shrubby seral stages of communities in the Helderberg Plateau region of New York]. However, *there is an expected pattern of higher densities of birds in mature forests in the deciduous forest biome.*

Relationship between Avian Succession and Plant Succession

The general pattern of avian succession is considered by several authors to be a manifestation of the habitat preferences and ecological requirements of the bird species (e.g., Kendeigh, 1945). Bond (1957) and Shugart and James (1973) have analyzed the correlation of bird and plant similarity coefficients (Austin and Orloci, 1966) between different communities. In both of the studies the correlations were found to be strong and statistically significant. The overall indication is that *the similarity in the vegetation in two areas (in the same region) is a reasonable index of expected similarity in bird communities.* Following observations made by MacArthur and MacArthur (1961) who found a strong correlation between bird species diversity and an index of vegetation structure (the foliage height diversity), Tramer (1969) speculated that the changes in avian communities were largely due to changes in vegetative layering of plant communities. Shugart and Hett (1973) compared the turnover rates of different communities and found that the bird species composition of a community changed more rapidly than the plant species composition (although the pattern of change was the same between plants and birds).

Patterns of Avian Energetics

There have been a limited number of studies in deciduous forests which have elaborated the energetics of the bird communities. Karr (1971) found a general increase in bird standing crop and existence energy as the ecological age of abandoned strip mines increased. Using information provided by Mrs. Shirley Marshall at the University of Georgia (personal communication) and Stewart and Skinner (1967), we converted the Shugart and James (1973) avian community succession data from Arkansas to kcal per 100 acres (Fig. 3). *The general pattern of bird standing crop is the same as the pattern of bird density.* This observation indicates that the average size of breeding birds does not fluctuate widely through this successional sequence. There are two exceptions; in the ecotonal stages the size of birds tends to be larger on the average (A, Fig. 3) and in the mature forests the mean size appears to be somewhat smaller (B, Fig. 3). The correlation between bird standing crop and density is also evident in studies by Karr (1971) and Sturges et al. (1974).

RESOURCE DIVISION AND HABITAT SELECTION

Schoener (1974) has recently reviewed the underlying ways that similar species utilize different resources in their environments, and identified the following important considerations relative to birds:

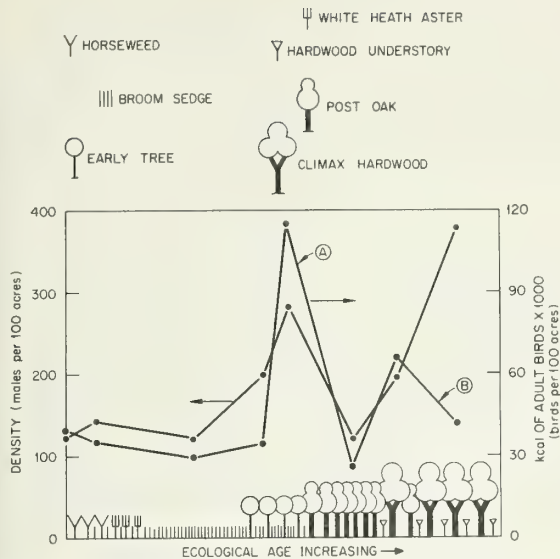


Figure 3.--Density and standing crop of bird life for an Arkansas succession. Figure modified from Shugart and James (1973).

1. In considering the important particular dimensions in resource partitioning, *habitat dimensions are more important than food-type dimensions* which are, in turn, more important than temporal (time of day of feeding, etc.) dimensions.

2. As the number of species considered increases, so does the number of important dimensions in resource division.

Recently, there have been multivariate statistical analyses (James, 1971; Shugart and Patten, 1972; Anderson and Shugart, 1974) directly applied to determine the influence of a number of habitat variables on the distributions and microhabitats of entire avian communities. These studies indicate that the simple relationship between bird species diversity and foliage height diversity first presented by MacArthur and MacArthur (1961) is neither as direct nor as universally applicable as it was first thought. The application of multivariate analysis to the habitat selection problem in birds also seems to reduce problems in data interpretation.

As an example of this general approach to avian habitat selection and to demonstrate the potentials of multivariate analyses as a management tool, we will document in some detail the resource division/habitat selection of seven common species on Walker Branch Watershed (located on the U.S. Energy Research and Development Administration - Oak Ridge Reservation in eastern Tennessee). We will use a statistical technique

called multiple discriminant function analysis (Cooley and Lohnes, 1971) to describe the importance of habitat, feeding behavior, and food for each of these species. A discriminant function can be thought of as a combination of some set of variables that is statistically maximal for separating groups. In the present case, a discriminant function in an index (albeit a rather sophisticated index) that accentuates the differences in habitat preference, food articles, and feeding behaviors among seven common song birds. A more detailed discussion of the ecological theory and implications of discriminant function analysis may be found in Green (1971, 1974). Considering the percentage of time spent in various food-gathering activities (e.g., leaf-gleaning, trunk-gleaning, hawking insects) as variables to be used in determining differences in the seven bird species, we determined a behavioral discriminant function (Fig. 4, horizontal axis). Similarly, considering the portion of the seven bird species' diets composed of different identifiable food types (in this case about 40 categories including insect taxa, vegetative plant parts, etc.), a food discriminant function was calculated (Fig. 4, vertical axis).

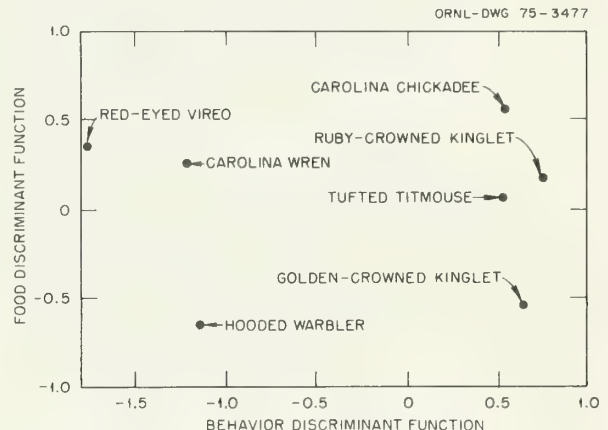


Figure 4.--Food and behavior discriminant functions for seven bird species common on Walker Branch Watershed. Names of the seven species are listed on the figure.

By plotting the verage behavior and food preferences of the seven birds, several patterns emerge. The Kinglets, Tufted Titmouse, and Carolina Chickadee are found to have very similar feeding behaviors (note similar mean values on behavior discriminant function) but rather different food preferences. This group of bird species (often referred to as a guild) are frequently found feeding in mixed flocks. The two ground feeding bird species considered (the Hooded Warbler and the Carolina Wren) also have similar behaviors but different food preferences. The Red-eyed Vireo, Carolina Wren, and Ruby-crowned Kinglet all have similar foods but use

different foraging behaviors to obtain these foods. A similar pattern holds for the Hooded Warbler and the Golden-crowned Kinglet.

In the case of the discriminant function analysis of behaviors and foods of the seven bird species, we have demonstrated the use of a multivariate analysis technique to parsimoniously describe differences in the natural history of these species. Along with the descriptive power of this technique (consider the difficulty in demonstrating the patterns listed above had we listed percent of time spent using each of 12 different feeding activities in each of seven bird species; or 40 food types in seven species), the discriminant analysis technique also has potential as a management aid for non-game species. In an earlier paper (Anderson and Shugart, 1974), we attempted to demonstrate the use of discriminant function analysis in identifying the important habitat variables for each species in a breeding bird community. Figure 5 diagrams the habitat selection patterns for the seven bird species studied here as they change seasonally. The two discriminant functions were formed from 28 habitat variables (e.g., height of canopy, volume of leaves, thickness of understory) describing a microhabitat associated with individuals of each of the seven species. Multivariate axes are generally difficult to meaningfully

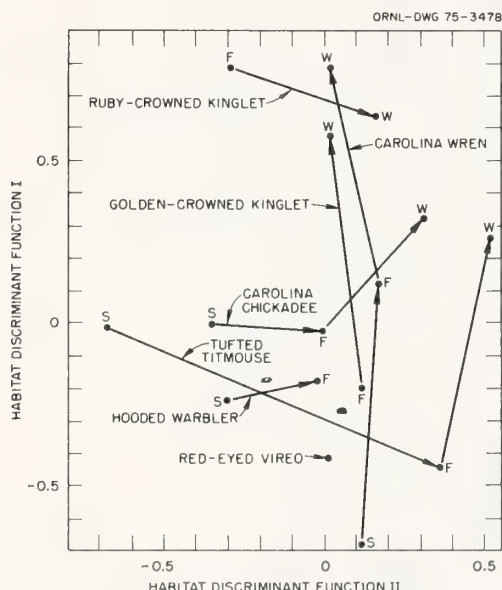


Figure 5.--Two discriminant functions (incorporating 28 habitat variables for habitat selection during three different seasons for seven bird species common to Walker Branch Watershed. S indicates summer; F indicates fall; W indicates winter. Each point is the mean habitat associated with each species in a given season. Species names indicated on figure.

verbalize, but the numeric value of discriminant function I tends to increase with the evergreenness of the forest site and the numeric values of discriminant function II tends to increase with the number of small trees on a site. Thus, in the summer (S on Fig. 5) the species typically are found in hardwood mature forests and as fall (F) and winter (W) arrive the species shift to less mature forest sites with more and more evergreen trees (Pines and Junipers).

Using analyses of this sort, a given location in a forest can be measured using the same habitat variables as were used in the microhabitat description and plotted as a point on a graph such as in Fig. 5. Thus, one could identify forest sites that are good Hooded Warbler habitat or are good wintering habitat for Wrens, or any number of other desirable attributes. These methods should be useful in optimizing management strategies for non-game birds and for identifying potential impacts of changes in management policies on birds.

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Plant Succession and Interactions with Fauna¹

Robert B. Hamilton and Robert E. Noble^{2/}

Abstract.--A literature search revealed that not much is known about bird populations in deciduous forest seres. Habitat management results in modifying, simplifying, and changing relative proportions of habitats. Avian variety and density is related to habitat type and complexity. To encourage birds by management, habitat variety and complexity should be emphasized.

INTRODUCTION

Our topic is about plant succession and bird populations in the deciduous forest. Another speaker will discuss bird populations and succession in the coniferous forest and a third will speak about avian populations on rangeland. We will concern ourselves with characteristics of bird populations in the deciduous forest sere and with the methods of managing nongame populations in these habitats. Our approach will primarily be one of a literature review but some of our own work will be used for illustration, where appropriate.^{3/}

The management information we will provide is primarily speculative; there has been little work done on management of nongame birds in these habitats or any other for that matter. However, there has been extensive work

on managing game birds in some wooded habitats and many non-wooded ones. What work that has been done on managing nongame birds has usually been incidental to other management objectives such as maximizing cellulose or game bird production. We will consider all birds in our presentation; biologically, game and nongame birds are the same. It will be seen that many present management practices can be considered somewhat harmful to avian variety and density.

There may be some overlap between this paper and others in the symposium. One cause of this is the variability in succession; another is the universality of some ecological generalizations. In some deciduous "seres" ("the whole sequence of communities that replace one another in a given area" [Odum 1971]) there are coniferous forest "seral stages" (the relatively transitory communities which are passed through on the way to the terminal stabilized community or "climax" [Odum 1971]) and in some coniferous seres there are deciduous forest seral stages. In both biomes there are seral stages which are regularly grazed. The subjects covered in this symposium are of concern to many land managers. There are bird populations in other climax communities such as chaparral, desert, etc. which could also benefit from consideration; where development is proceeding rapidly, study is especially important.

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Succession

"Ecological succession" or "ecosystem development": (1) is "an orderly process of community development that involves changes in species structure and community processes with time; it is reasonably directional and therefore predictable, (2) results from modifications of the physical environment by the community..., (3) culminates in a stabilized ecosystem in which maximum biomass... and symbiotic function between organisms are maintained per unit of available energy flow" (Odum 1971).

Odum (1969) discusses theoretical trends that can be expected in succession. The most important trends for our consideration are: (1) variety component of species diversity increases i.e. number of species increases, (2) equitability component of species diversity increases i.e. there tends to be a more even division in numbers between individuals of the various organisms in the community, (3) stratification and spatial heterogeneity increases i.e. more niches become available, (4) niche specialization increases, (5) size of organisms increases, (6) biomass increases, and (7) gross production/community respiration (P/R ratio) decreases and approaches one. All of the above results in the complication of food webs and an increase in stability in the system (De Angelis 1975).

There is an inherent conflict in these trends, and our desire to manage avian populations. By necessity most avian management has been incidental to other aims such as timber or pulpwood production. As an ecosystem matures P/R decreases. In other words, no new net biomass is added. Therefore, harvesting will tend to be accomplished when the net increment of biomass increase begins to decrease (fig. 1). This is at a time when the variety of bird-life has not yet reached its maximum and would be in conflict with a desire to maximize avian variety in that stand. We will talk more about this problem later.

Succession in the Deciduous Forest Sere

As has been stated previously, succession in the deciduous forest biome (we use this term to describe the area vegetated at least historically by the deciduous forest sere) is a complex phenomenon involving changes in species composition stratification and species diversity of both plants and animals. There are two types of succession: "primary" and "secondary." "Primary succession" is suc-

sion on land that previously was not vegetated. "Secondary succession" is succession on land that has been previously vegetated but that has been cleared for some reason. Primary succession usually takes much longer than secondary succession to be accomplished, especially in the initial stages, because more dramatic changes must be made to the environment in order to make it suitable for the next seral stage. These changes usually involve the build up of soil suitable for the incoming vegetation.

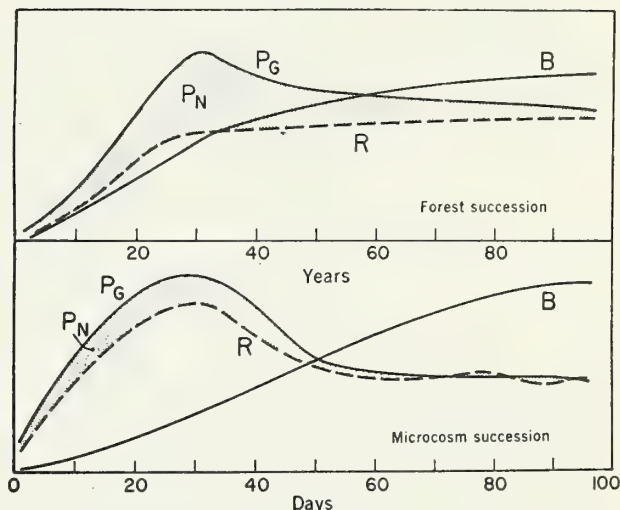


Figure 1.--Comparison of the energetics of succession in a forest and a laboratory microcosm. P_G , gross production; P_N , net production; R , total community respiration; B , total biomass. (Odum 1969)

We are mostly interested in "secondary succession," since this is the type of succession which we ordinarily manage. Very little "primary succession" is now occurring. Furthermore, the later stages of "primary succession" tend to be similar to "secondary succession" and it is the later stages that we are interested in; the two are practically the same for our purposes.

A typical scheme of plant community succession that occurs in the deciduous forest biome is shown in figure 2. This is a diagram of "secondary succession" or "old-field succession" in the Piedmont Region of Georgia. Old-field succession is similar in many upland areas of the Southeast. The trend is from a bare field initially colonized by low annuals through perennial grassland and shrub stages up to a pine forest which is ultimately replaced with a shade tolerant deciduous forest. In some areas of the Southeast the deciduous forest does not occur because periodic fires (either natural or man-set) destroy the deciduous tree seedlings but do relatively little

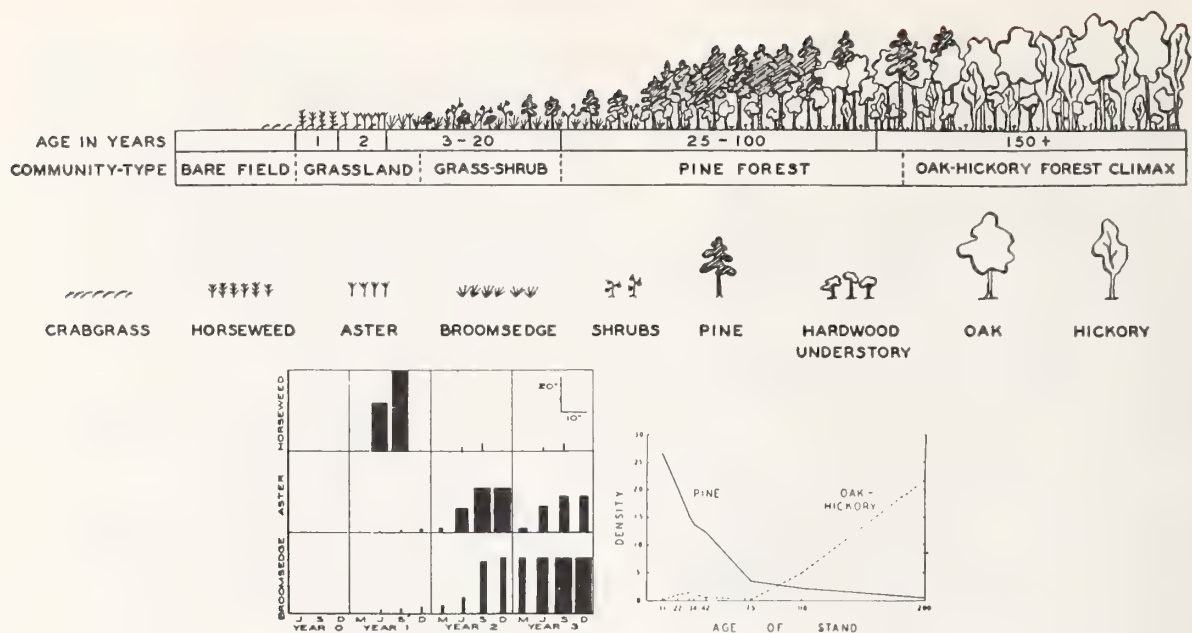


Figure 2.--Secondary succession on the piedmont region of southeastern United States. The principal plant dominants of the upland sere which follows abandonment of crop land (cotton, corn, etc.) are shown in pictorial fashion in the upper diagram (after E. P. Odum). The lower charts contain quantitative data. On the left, the relative size of the three pioneer plants which reach dominance in successive years, namely, horseweed (Leptilon = Erigeron), aster (Aster), and broomsedge (Andropogon), is depicted (after Keever, 1950), while the gradual change from pine to hardwood dominance is indicated on the right (after Oosting 1942). In the diagram at left, depicting relative size of the three plants, height of the columns represents average height of plants in inches, and width of columns represents relative diameter of stems. In the diagram at the right, the density figures are number per 100 m². (Johnston and Odum 1956)

permanent damage to the fire-tolerant pines. Of course, the usual changes in succession such as an increase in stratification as shown in figure 2 are also occurring. As the vegetation changes, corresponding changes in bird populations are occurring. It is these changes and the reasons for them that will concern us here.

Alternate schemes of succession in the deciduous forest occur. There are coniferous forest successional stages in many deciduous forest successional schemes; on the other hand, there are deciduous forest successional stages in coniferous forest succession.

We will concentrate our attention on general trends of succession and will not worry about the details of which avian species are characteristic of which successional stages. We will, however, discuss briefly some species characteristic of various deciduous forest seral stages.

Given above are some of the typical schemes of secondary succession. The scheme is quite different when man begins to manage the forest. Man, in general, attempts to

compress or eliminate succession as much as possible in order to obtain a desired crop as soon as possible and to maximize profits. In the deciduous forest biome of the Southeast man frequently manages for pine production -- thus managing for a subclimax successional stage. Succession is artificially culminated by harvesting of the pine forest, then clearing the ground in some way, and starting a new successional process. Early stages are by-passed or compressed by planting of seedlings or direct-seeding. Understory is discouraged by various site preparation techniques and that which develops is removed as quickly as possible with fire or some other convenient management tool. The net effect of all this is to greatly reduce or eliminate some of the successional stages and their associated fauna. This results in an overall decrease of variety in the environment. Since the lumber is harvested before the ecosystem reaches stability, man continually has to interfere in the process to produce the desired results. The type of interference such as application of fertilizer, weed killer or insecticide often results in unwanted environmental effects elsewhere. In other words, we are managing for production, not stability. Only in a

stable ecosystem could management be minimized.

THE BIOME CONCEPT

In an effort to organize information about plant and animal communities several classification schemes have been proposed. These include "biotic provinces," "life zones," and "biomes." The "biome" is equivalent to the "plant formation" of plant ecologists except that "biome" is used to describe the entire community and not just the vegetation. It is the largest land community which is convenient to recognize (Odum 1971). The life-form of the dominants of the "climatic climax" (regionwide similar climax due to similar regionwide climatic patterns) is uniform. Included within the "biome" are not only the climatic climax, but the "edaphic climaxes" (variations of climax due to peculiar local conditions such as soil type) and seral stages as well.

Although the "biome" concept is widely used it is not of great use to us since the distribution of birds is different in all the seral stages of the "biome." In fact, Pitelka (1941) showed that there is no relation of birds to specific dominants or group of dominants, but there is a relation between bird species and life forms of plants. Instead he says, "a clearer understanding of the facts of bird distribution can be obtained through an appreciation of the laws of biotic succession and recognition of developmental as well as climax biotic communities over the continent".

Bond (1957) said "The importance of the life form and physical features of the habitat in the distribution of birds, the occurrence of similar bird species in similar life form situations in different biomes, the indistinctness of boundaries between units, all suggest that the unitary nature of community categories should be questioned."

James (1971), Anderson and Shugart (1975) and Whitmore (1975) among others have studied the niches of birds by complex multivariate statistical techniques. Their results were an ordination of bird species along complex statistically arrived at environmental gradients. Their approach is inconsistent with the "biome" concept but seems very useful in explaining bird distribution. Modern niche theory is also somewhat contrary to the biome concept.

Therefore, it is more difficult to explain the distribution of avian communities than simply looking at a map.

BREEDING BIRD DIVERSITY

When considering bird communities several concepts have been used to condense community data into a single number. The most used concept to accomplish this is that of "species diversity." This concept takes into account both the number of species present ("species richness" or "species abundance") and the evenness that occurs between the number of individuals of each represented species (Margalef 1958, Pielou 1966). The currently most popular index of species diversity is derived from information theory and is calculated by the formula (Shannon and Weaver 1963):

$$H' = -\sum_{i=1}^N \frac{N_i}{N} \log \frac{N_i}{N}$$

when H' = species diversity index

N = total number of individuals of all species

N_i = number of individuals of the i^{th} species

Hurlbert (1971) makes a convincing argument that this formula is meaningless ecologically and that formulas should be used that have biologic meaning (e.g. probability of interspecific encounter). We are in basic agreement with Hurlbert; however, others have used H' to describe avian communities or to make comparisons between habitats and we find it convenient to use their data or generalizations (in some cases we calculate H' for our data to use in the same comparisons). Tramer (1969) showed that in birds H' was highly correlated with species richness ($r = 0.972$); relative abundance was stable in his samples. Therefore the generalizations made by comparing H' values should be the same as generalizations from species counts.

When comparing H' values it must be realized that H' varies with sample size. Some (Sanders 1968, e.g.) have attempted to derive a correction for sample size but have been unsuccessful (Fager 1972). Wilhm (1970) showed, however, from progressively pooled samples in 13 habitats that diversity reached an asymptotic value with increased sample size.

Another problem with all bird community data is that the censuses on which they are based in many cases probably are not true censuses and may not always be accurate. However, these are the best numbers that we have. We will not discuss this problem here, but methods of assessing bird populations efficiently warrant further investigation.

Bird species diversity changes in relation to plant succession (Margalef 1963, 1968; Karr

and Roth 1971; Odum 1969; Karr 1968; Recher 1969; and many others). Bird species diversity is also the most variable where the ecosystem is the least complex and therefore the least stable (Kricher 1973). In plant succession the earliest seral stages are structurally the simplest and the most unstable, while climax is the most stable and complex seral stage (Odum 1969). Therefore, bird species diversity is lowest in very early seral stages, higher in later seral stages and highest at climax. Kricher (1973) states, "As [plant] succession continues, the degree of instability, as measured by the rapidity of change in the biotic components, decreases steadily."

THE EDGE EFFECT

The tendency for increased variety and density at community junctions is known as the "edge effect" (Odum 1971). In Texas a study of woodlands and associated clearings revealed that margins had 95% more birds representing 41% more species than corresponding areas of woodland (Lay 1938). In a study of breeding passerine birds in a secondary upland sere of the Piedmont Region of Georgia, Johnston and Odum (1956) found that about 40% (20/50) of the common species could be considered primarily edge species; 13 of these species were never recorded on uniform study areas. Verna Johnston (1947) in a study of deciduous forests in Illinois classified 14 bird species as edge species and 10 as interior species. Four species were classified as both; the male Ruby-throated Hummingbird (*Archilochus colubris*) was classified as an edge species but the female as an interior species. She concludes that the forest edge is a distinct community because it is inhabited by a unique fauna.

Not only the species present but their densities show an "edge effect". Beecher (1942) compared breeding bird densities in a large block of habitat with an equivalent acreage composed of small blocks. He found that population density increased with the increase in relative amounts of edge. In an artificial habitat around a small village in California, Pitelka (1946) found a density of approximately 12 pairs/acre. (We found a similar density in an area which consisted mostly of edge-like situations in the forest). Johnston (1970) found a density of approximately 800 pair/100 acres in a mature upland deciduous forest (compared to normal densities of 100-400 pair/100 acres [Kendeigh 1961]); he attributed the high density to a planted shrub layer and openness which created a relatively large amount of edge.

BIRD COMMUNITIES AND SUCCESSION

Because birds are migratory and many of the forms that we find in the various seral stages are not permanent residents, it is not convenient to speak of bird communities in general. Rather we must speak of at least three different avian communities: birds present in the summer and breeding or presumed breeding; birds spending the winter; and the community of migrants that pass through in spring or fall. These communities are not completely separate but may consist of many of the same individuals and species. Many individuals may be permanent residents and thus may be part of both the breeding community and wintering bird community, for example. We have 411 bird species on Louisiana's state list. Only 98 of these are permanent Louisiana residents. Forty-nine species occur only as breeding birds in spring and summer; 120 species nest elsewhere but winter in the state, and 59 species are transients passing briefly through Louisiana to and from their northern breeding range and their wintering grounds in Central and South America. The remaining species are vagrants that have occurred in the state only occasionally. Consequently, depending upon season, there are, on any of our study areas in Louisiana, a permanent resident bird community, a breeding bird community, a wintering bird community, and a community during migration in spring and fall which includes a combination of the above mentioned communities plus the transients.

These three distinct communities, all occurring within the same seral stages, albeit at different seasons of the year, are represented to some extent by different species and densities. As an example the deciduous forest of Louisiana support about twice as many wintering birds as they support breeding birds (Dickson 1974, p. 111) in early spring.

Plant succession determines what bird species are present and in what numbers, but it is important to remember that species composition and numbers change with season. For that reason one generally restricts his discussion to the breeding bird community and/or the wintering bird community of any given area.

Most discussion of avian communities in various habitats are concerned with breeding populations or communities and by necessity our discussion will primarily deal with this type of community. We will discuss the other types of communities briefly also.

Studies so far seem to indicate two primary factors to account for avian species diversity in deciduous forests: foliage height diversity (foliage measure of cover, usually at three heights in a stand corresponding to herb, shrub and canopy layers) and horizontal diversity within a foliage level (MacArthur and MacArthur 1961, MacArthur 1964). Avian species diversity seems to be positively correlated with foliage height diversity (MacArthur and MacArthur 1961), and since the number of levels and thus the foliage height diversity tends to increase as succession increases, avian species diversity also tends to increase. Thus maximum species diversity is usually achieved at or near climax (Karr 1971; Shugart and James 1973 e.g.). Sometimes, there is a slight decrease of diversity at climax (Karr 1971 e.g.). We know of no study that explains this decrease but it is likely to be due to a small loss of foliage height diversity at lower levels because of shading after canopy closure. There have been several studies showing the relationship between avian species diversity and foliage height diversity; these studies usually indicate a positive linear relationship when plots of the same size are used (fig. 3).

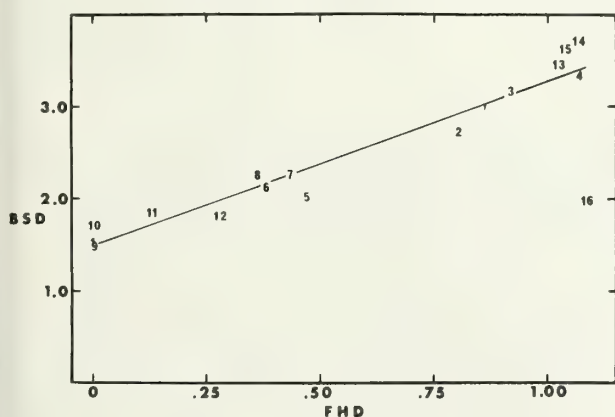


Figure 3.--Linear regression of bird species diversity (BSD) on foliage height diversity (FHD) for pooled Illinois (1-4), Texas (5-8), and Panama (9-15) data (Bahama Pine Forest - 16). (Karr and Roth 1971)

Connell and Orias (1964) warn, however, "we feel that although some niches are determined by physical variations in the environment, most of the dimensions of the niche are a result of interaction between organisms. For this reason, it is impossible to predict the number of niches (and therefore species) from environmental complexity alone." The

known latitudinal gradients (Cook 1969, Tramer 1974) of species diversity cannot be explained by simple increases of foliage height diversity. Other factors must be involved. Tomoff (1974) found that physiognomic coverage diversity was also important in desert scrub communities.

In addition to the increase in species diversity with succession there is a gradual change in species composition between seral stages (table 1). This is brought about primarily because of changes in life forms of the constituent vegetation. Therefore, the total variety of avifauna in a sere is much greater than the variety in any particular seral stage. This has to be taken into account in any management scheme. In addition to the increase in diversity there is an increase of avian density with succession. For maximum bird density within a stage therefore late successional stages should be favored (fig. 4).

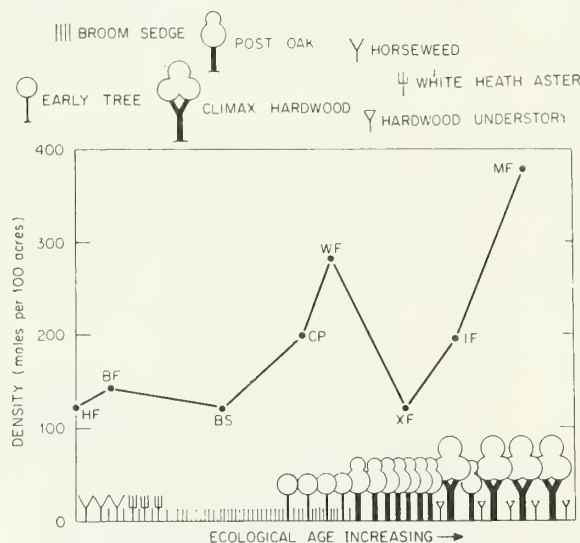


Figure 4.--Density of birds expressed in territorial males per 100 acres in various stages of plant succession. Dots represent study plots. HF = mowed hay field plot; BF = burned field plot; BS = broom sedge field plot; CP = clonal persimmon field plot; WF = woody field plot; XF = xeric forest plot; IF = intermediate forest plot; MF = mesic forest plot. (Shugart and James 1973)

Most studies reveal that the precise species of plants involved is not important in what species of birds are present but rather their life form (Pitelka 1946, Bond 1957, James 1971, Whitmore 1975). Since the life forms in seral stages are not nearly as variable as the species composition, the precise vegetative composition of the vegetation is not particularly important when considering avian communities. However the Louisiana Waterthrush (*Seiurus motacilla*) requires a

Table 1.--Distribution of breeding passerine birds in a secondary upland sere, Piedmont Region, Georgia. After Johnston and E. P. Odum (1956). Figures are occupied territories or estimated pairs per 100 acres.

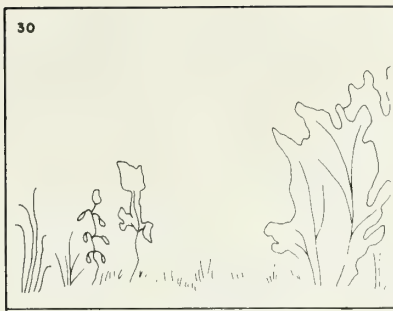
Plant Dominants Age in Years of Study Area	Forbs		Grass-shrub			Pine Forest		Oak-Hickory Climax,	
	1-2	2-3	15	20	25	35	60	100	150-200
<i>Bird Species (having a density of 5 or more in a given stage) †</i>									
Grasshopper sparrow	10	30	25						
Meadowlark	5	10	15	2					
Field sparrow			35	48	25	8	3		
Yellowthroat			15	18					
Yellow-breasted chat			5	16					
Cardinal			5	4	9	10	14	20	23
Towhee			5	8	13	10	15	15	
Bachman's sparrow				8	6	4			
Prairie warbler				6	6				
White-eyed vireo				8		4			
Pine warbler					16	34	43	55	
Summer tanager					6	13	13	15	10
Carolina wren						4	5	20	10
Carolina chickadee						2	5	5	5
Blue-gray gnatcatcher						2	13		13
Brown-headed nuthatch							2	5	
Wood pewee							10	1	3
Hummingbird							9	10	10
Tufted titmouse							6	10	15
Yellow-throated vireo							3	5	7
Hooded warbler							3	30	11
Red-eyed vireo							3	10	43
Hairy woodpecker							1	3	5
Downy woodpecker							1	2	5
Crested flycatcher							1	10	6
Wood thrush							1	5	23
Yellow-billed cuckoo								1	9
Black and white warbler									8
Kentucky warbler									5
Acadian flycatcher									5
Totals: (including rare species not listed above)	15	40	110	136	87	93	158	239	228

small stream, the Northern Parula (*Parula americana*) needs Spanish moss and the Worm-eating Warbler (*Helmitheros vermivorus*) requires a steep hillside. Anderson and Shugart (1974) demonstrated that Downy Woodpecker (*Dendrocopos pubescens*) abundance was correlated with the number of saplings in a stand. Most, if not all species do have unique requirements but these requirements do not have to be so unique that they cannot be found in many stands of an appropriate habitat (see fig. 5 for "representative" habitat requirements of some deciduous forest birds). Therefore any particular stand will have niches available for many different species.

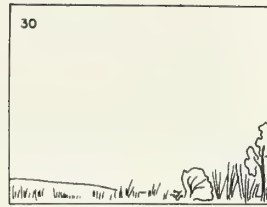
WINTER BIRD COMMUNITIES

Most studies of avian communities ignore this important element. Consequently, there is not much published literature to which we can refer. We have gathered together some of the data we have generated in various studies to compare breeding bird and winter bird communities. Surprisingly enough, avian species

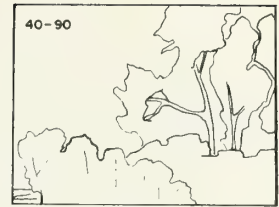
diversity is not greatly reduced in the winter (fig. 6). We have not actually measured foliage height diversity in the winter in the deciduous forest but because of leaf-fall it must be considerably less in the winter than during the breeding season. At the same time, because of the colder winter weather, the availability of exposed insects must be greatly reduced so that many insectivorous niches available in the breeding season will no longer be available. For both of these reasons we would expect a greatly reduced avian species diversity during the winter. The only explanation for the comparable species diversity, with it being higher in winter in some areas, is the narrowing of old niches and the opening up of new niches which often consist of reservoirs of edible biomass that have accumulated on or near the ground through the action of gravity on edible matter produced above ground level, or of food matter protected by favorable microclimates in the litter layer of the soil. Much of the food produced during the year, such as seeds, is not consumed immediately but is utilized later. Since many of these high-energy food packets



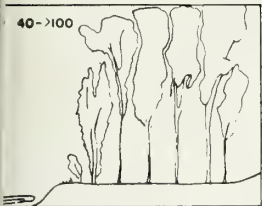
BELL'S VIREO



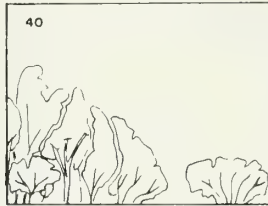
YELLOWTHROAT



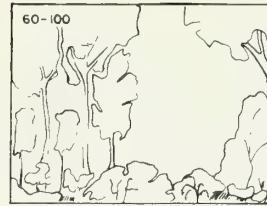
REDBLACK



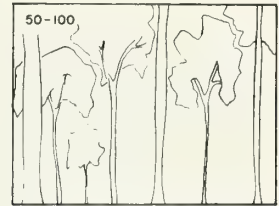
WARBLING VIREO



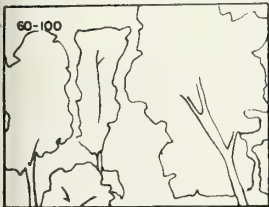
WHITE-EYED VIREO



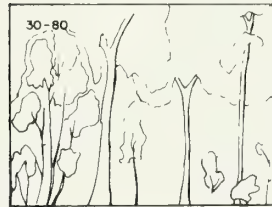
HOODED WARBLER



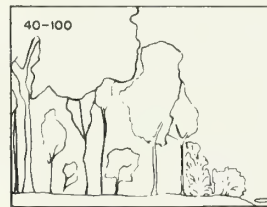
BLACK-AND-WHITE WARBLER



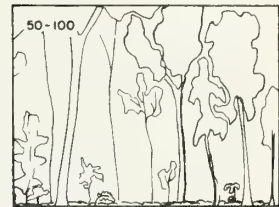
YELLOW-THROATED VIREO



RED-EYED VIREO



PARULA WARBLER



OVENBIRD

Figure 5.--Outline drawings of the niche-gestalt for five species of vireos and six species of warblers, representing the visual configuration of those elements of the structure of the vegetation that were consistently present in the habitat of each. Numbers give the vertical scale in feet. (James 1971)

have evolved as propagules, enough have to be produced on the average for some to survive long enough to germinate, grow and reach maturity. Most plant propagules will reach unfavorable sites or be consumed and therefore a great excess of these structures are produced. Many of the wintering birds subsist on these; others, however, still subsist largely on overwintering insects or their larvae.

Bird numbers reach their peak at the end of the breeding season and then decline slowly until the beginning of the next breeding season. Therefore, it is expected that the average density of birds will be higher in the early winter than in the spring (table 2). This abundance pattern is complicated by migration patterns but on the average, since migration reduces the average area utilized by birds, the winter increase in density should

be enhanced. Therefore, we expect in many, if not in most ecosystems, rather high winter bird densities (a further complication is the reversal of seasons at the equator and the fact that many birds migrate across the equator thereby always staying in summer conditions). Because of the high winter densities and the relatively low biomass production during this season, as well as the relatively low temperatures resulting in high food demands and sometimes at least in deaths to individual birds that have not found the proper shelter, winter can be a crucial time to many bird species. It is unfortunate that it has been largely ignored in the study of bird communities. If a bird species has relatively specialized winter habitat requirements, a loss of winter-habitat can be just as detrimental as a loss of breeding habitat.

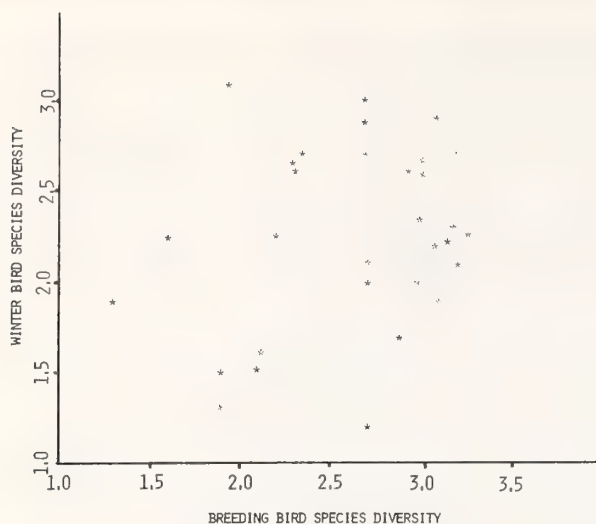


Figure 6.--Comparison of H' for summer and winter populations in various deciduous forest habitats. (H' values at each point represent one area reported in both a Breeding Bird Census and Winter Bird Count in American Birds).

Table 2.--Breeding-bird and wintering-bird populations, per 100 acres, in pure, even-aged, loblolly pine forests of three age-classes and a "control." Livingston Parish, Louisiana 1974-1975.

Forest stand	Breeding bird population	Winter bird population
6-year old Loblolly Pine	268 (9)*	289 (31)
20-year old Loblolly Pine	148 (9)	154 (21)
46-year old Loblolly Pine	234 (16)	137 (23)
Control	1254 (18)	686 (31)

*Number in parentheses is the number of species constituting the population.

TRANSIENT BIRDS--A SPECIAL PROBLEM

We generally know the seral stages preferred by breeding and wintering birds of a given area but we know very little about the habitat requirements of transient birds. Mangnolia (*Dendroica magnolia*), Cape May (*Dendroica tigrina*), and Blackburnian Warblers (*Dendroica fusca*) plus other species pass through Louisiana in spring and fall migrations. These warblers nest in coniferous

forests of the far north. In passing through Louisiana they stop in large numbers to feed and rest in our chenier woods, bottomland hardwoods, and other forest types. These birds can hardly make a trans-Gulf flight during inclement weather (Lowery 1974, p. 75) and then continue across Texas or Louisiana to stop many miles inland. Just how important are the chenier woods and other forest stands near the Gulf as a resting and feeding area for trans-Gulf migrants? What effects do various silvicultural practices have on these birds? Will or can Scarlet Tanagers (*Piranga olivacea*) use clearcuts or pure, even-aged forest stands for resting and feeding in migration? We do not know. But possibly some, most, or even all transients require certain seral stages for resting and feeding in migration. Extensive habitat manipulation on a large scale under such circumstances could reduce the numbers of certain birds with no changes having occurred in either their preferred nesting habitat or their preferred wintering habitat. This is a field that demands investigation.

The question is how labile are habitat requirements during migration. Many incidental observations certainly confirm that in general most birds utilize habitats at least superficially similar throughout the year. One does not find tanagers in alfalfa fields during migration or Grasshopper Sparrows (*Ammodramus savannarum*) in the forest. Robert J. Newman (personal communication) reports that many of the transgulf migrants leaving Yucatan do not leave from the coast which is mostly agricultural land or scrub but rather leave from the thickly forested interior of the peninsula. This lengthens their trips, thereby increasing the danger; and probably indicates somewhat inflexible habitat requirements in Mexico. We do not see why the requirements would not be just as inflexible in the United States.

If habitat requirements are inflexible then we should expect it to be desirable to have at least islands of suitable habitats available for occasional use of migrating birds. This would be especially important in areas where birds would land after extended flights--areas like the north coast of the Gulf of Mexico.

TRENDS IN THE DECIDUOUS FOREST BIOME

Originally the majority of the eastern United States was a deciduous forest. The exact pattern was a mosaic with forests of different character at high and low elevations and also with forest types varying with latitude

and local conditions. Depending on details of history, such as patterns of fire, there were patches of various successional stages scattered throughout. The extreme southeastern part was occupied predominantly by a fire-maintained pine-forest. We have no idea of the relative proportion of climax vegetation as opposed to the quantity of habitat in the various successional stages but the climax must have been predominant. All was not climax, however, as fire and wind damage periodically put the forest back to an earlier successional stage (if it were all climax, those species confined to early seral stages would have become extinct). Fire was caused both by lightning and purposely set by Indians. In John James Audubon's extensive travels throughout the region he only saw one Chestnut-sided Warbler (*Dendroica pensylvanica*) and Alexander Wilson only reported one Mourning Warbler (*Oporornis philadelphia*) from his travels in the region (Griscom and Sprunt 1957). Both of these Warbler species are restricted to brushy successional stages.

Today, if we fly over this area we find relatively small proportions of climax forests or forests of any type for that matter. Instead most of the land is now managed by man--for agricultural production. Figure 7 shows these trends in Illinois which we assume is typical of other states. Today most of the forests have been removed from much of the elevated flat lands and the forests remaining are restricted to strips along the major water courses and the mountains and hills unsuitable for agriculture for one reason or another. It probably can be said that most of the deciduous forest that now exist are present on lands not suitable or marginally suitable for agriculture at the present time. Even where forests exist today they are not the virgin

forests that were present when the country was settled but rather are areas of second and in some cases third growth.

In many places our upland deciduous forests are being replaced with pine-forests (often monoculture pine) and our bottomland forests are either being flooded by new reservoirs or being drained and diked and planted with crops such as soybeans or occasionally planted with monoculture cottonwood or sycamore.

Habitat Destruction

Habitat destruction has been widespread and will undoubtedly continue as man manages more and more of the earth's surface for his immediate benefit (or what he perceives to be for his benefit). We see no need to document the extent but changes have been considerable. For example it has been said that when this country was settled a squirrel could travel in the Eastern Deciduous Forest from the Atlantic Ocean to the Mississippi River without ever touching the ground (Smith 1966). This is certainly an exaggeration but does give an indication of the original extent of our deciduous forest.

Graber and Graber (1963) compared the bird populations of Illinois in 1956-1958 with the populations there earlier. (Illinois is probably representative of the country with respect to these trends.) They noted both a decrease in total number of birds and in diversity. There has been a recent trend of increasing bird numbers confined to a few species associated with managed habitats.

Forms restricted to endangered habitats are endangered forms. If the habitat becomes ex-

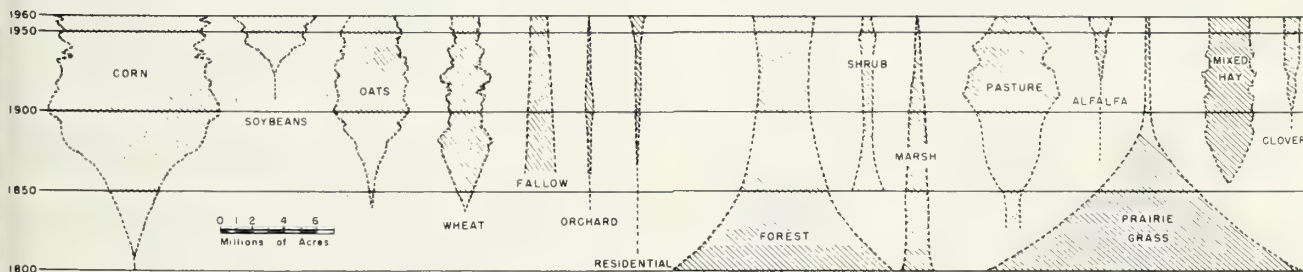


Figure 7.--Acreage of various bird habitats in Illinois from about 1800 through 1960. Acreage data are principally from four sources: published records of the United States Bureau of the Census, published records of the Illinois Cooperative Crop Reporting Service (Ewing 1959), published wetlands survey of the U.S. Fish and Wildlife Service (Shaw & Fredine 1956), and published records of the University of Illinois Agricultural Experiment Station (King & Winters 1952). (From Graber and Graber 1963)

tinct the characteristic forms will become extinct. Therefore, we should be careful to preserve representative habitats in order to maintain forms characteristic of them. This is now legally required by the Endangered Species Act. Diamond (1973) showed that in tropical forests there is a positive relationship between the area occupied by birds and the number of bird species present. He was dealing with a tropical situation but it certainly is true that any refuges that we establish should be large enough to support meaningful populations of all characteristic fauna. These populations should be large enough to maintain genetic diversity; ideally refuges of similar habitat types should be connected to allow gene flow in minimally mobile forms. Bond (1957), when analyzing responses of birds to different sizes of woods, showed that some species were more common in small woods while others were more common in larger woods. Oelke (1966) proposed four generalizations about the effects of block size on avian populations: (1) the larger the area of a habitat, the lower the density and nearer the density is to a limiting value; (2) the greater the number of layers in a habitat, the higher the density; (3) the larger the area of a habitat, the higher and nearer a limiting value the absolute number of species; (4) the larger the area of a habitat, the lower and nearer a limiting value the relative number of species.

In addition to destroying some habitat types, management also encourages rapid habitat changes, which favor genetically labile or colonizing species that are pre-adapted for fluctuating habitats. Those forms that are less plastic in their requirements will probably be selected against. This too will result in a decrease in diversity and should be avoided.

The best way to have maximum bird species diversity is to have maximum habitat diversity with all habitats preserved in reasonable quantity and in favorable geographic locations. This cannot be accomplished haphazardly and judicious planning will be necessary on the national and international level.

FUTURE USES OF OUR FOREST LAND

The demand for timber in the U.S. should be greatly increased by the year 2000 (U.S. Forest Service 1973). Any timber harvested by the year 2000 must be in the ground now or soon. It is also probable that the acreage devoted to timber production will be less by the year 2000 (10 million acres less in the

South by the year 2000 [Southern Forest Resource Analysis Committee 1969]). To produce more cellulose on less land will take intensive management. If this management is not well considered negative effects on avian populations will result.

Future demand for cellulose production is going to be high, but just how high would be especially difficult to ascertain now. With the recent trend in petroleum availability and the resultant concern with energy availability, especially within the continental United States, it is certainly very conceivable that energy and material production sources in the future will be from renewable sources such as our forests, and even higher goals may be imagined (the higher the goal the more intensive the management that is likely to be practiced--with the resultant impacts).

Other future trends are also likely to result in further pressure on our forests and forest resources. The human population in the world will be almost double its present level of approximately 4 billion by the year 2000 (Smith 1972). Even the United States will have an estimated population of between 250 and 300 million by then as opposed to a June 1974 population of approximately 211 million people in this country (U.S. Bureau of Census). This will result in the above mentioned demand for energy, cellulose, and other forest products. In addition, maximum effort will be required to feed all of these people. More cropland will be required to produce this food. Some of this cropland may come from cutting the forests (most suitable areas have already been cut); much in the past has come from this source. The modern "green revolution" which maximizes food production is accomplished by converting energy from fossil fuels to energy of food. Fossil fuels are becoming scarcer and possible replacements such as alcohol or charcoal from wood products for energy production can be foreseen. Transporting food to the hungry people of the world will also require additional energy. Alternate lower energy food production schemes are probably out of the question at this time because they produce much smaller quantities of food/acre.

In essence then the population explosion will result in much higher demands for food, fiber, and energy. Supplies of fossil fuels are becoming more unreliable, and the future seems to be a time of great pressure on our resources--forests and otherwise.

Besides the highly increased management needs in our forests and the reduced forest acreages there will be an increased demand for recreational resources. Methods must be

found to manage forests for increased production and at the same time provide recreational uses. Large populations of bird species and increased foliage and stand diversity are characteristics that enhance recreational use of forests.

This demand for recreational use is somewhat in conflict with the demand for greater fiber production. A manager would not take the same steps to maximize production as he would to maximize recreation. The ability of a manager to attain true multiple use will be strained to the utmost.

TIMBER MANAGEMENT IN DECIDUOUS FORESTS

There are two main trends in the management of forest ecosystems. One is the replacement of a natural forest ecosystem with another form of managed ecosystem such as crop ecosystems of various kinds and pasture ecosystems. The pasture ecosystems or similar range ones will be considered separately in this symposium but the agricultural ecosystems probably will not. We will consider agricultural ecosystems only briefly in this paper. The other trend is to manage the forest itself. This later strategy is the main one we will concern ourselves with here.

In the deciduous forest biome there are many successional stages. The forester will usually manage the forest to emphasize the stage that he perceives will produce the highest profit. In the Southeast this is usually the pine sub-climax. It is during this stage that the net accumulation of biomass is maximum (fig. 1). In relatively few upland sites are climax forests managed for timber production. (This is to be expected, as we saw earlier, because there is no net accumulation of biomass in a mature or overly mature climax forest.) Upland sites are usually managed for pine production at least in the Southeast. Often, if feasible, lowland sites are clear-cut and replaced by soybean fields--at least when levee protection is provided. In other sites American sycamore (Platanus occidentalis), Eastern cottonwood (Populus deltoides), or sweetgum (Liquidambar styraciflua) may be planted. In general the more favorable sites have been converted to crop or pasture production and the poorer sites are left for forest production.

In the current practices of forestry much of the management is monoculture management--managing for stands of one species of one particular age class. These stands may be of varying sizes or shapes. The total acreage devoted to any particular age class

will depend on the total land under management. If a sustained yield is to be maintained the total acreage of any particular age should approximately equal holding acreage/rotation age. Management then would be concerned with site preparation, planting, stand maintenance, and harvesting.

On some private lands and many federal lands, other management practices such as selection cutting also are used. Selection cutting and removal is exactly what the name implies, a selection of the trees to be cut and removed. This is difficult to accomplish without either down-grading or up-grading the stand; on some poor pine sites this method will probably continue to be practiced. As we have emphasized in many cases, where feasible, these stands will probably be replaced by monoculture stands, in the future, in order to maximize cellulose production. If this type of management is being practiced it is a simple matter to take wildlife consideration into account when the selection of trees to be harvested is being made. Of course, this is essentially a management of the climax vegetation. Succession will take place normally where the trees are removed. This creates more edge and if small clumps of trees are removed rather than individuals, the ensuing successional stages may be large enough to attract their characteristic avifauna.

On many private lands there is little or no management other than occasional cutting. On these lands a maximum of habitat diversity occurs. Incentive programs or other schemes to improve fiber production should be carefully considered or this source of habitat diversity will be decreased.

Management in national forests is like management as practiced by large timber companies except that multiple use considerations are supposed to be made. This has resulted in controversy as the champions of various special uses pressure for their desired usage to become predominant.

Much of the forests of our national parks have been managed as wilderness. This management tends to result in large areas of climax vegetation (unfortunately most of it second growth). These forests have been in some cases over-protected. Consequently the build up of fuel in some areas has been so severe that any fire now would result in a disaster. If normally occurring wild fire had been allowed, these stands would be more secure today. If we look upon national parks as a museum of our natural habitats, arguments can be made that all successional stages (not just climax) should be present and management

objectives would have to change.

In agricultural systems the natural trend would be for secondary succession to take place. These systems are maintained by constant cultivation. Large acreages of agricultural land are not very suitable for most breeding birds. Their numbers can be increased by interspersing woodlots, brushy fence rows etc. between the fields. These trends have decreased with modern "clean" agriculture and large corporate owned farms. The wholesale application of various insecticides, pesticides and fertilizers also often have detrimental effects on bird populations. The waste grain from modern agriculture has tended to have effects on winter-bird populations also. Large flocks of blackbirds are increasing in abundance in the winter. These flocks often number into the millions and can cause considerable damage and create a nuisance and health hazard in their roosting areas. There have been increasing tendencies and pressures to reduce some of these flocks.

OBJECTIVES FOR AVIAN MANAGEMENT

Non-game birds can be managed as well as game birds--in fact the management should be more simple since the managers do not have to worry about the setting of seasons or bag limits; however there are many more species to be managed and this itself is a complicating factor.

Avian management, in most cases, will of necessity be in conjunction with other management objectives since there is not likely to be a great monetary incentive for non-game bird management, and there are increasing pressures for the use of all suitable areas for food or fiber production or some other activity of man.

Like all management, however, it will not be easy. Sometimes difficult decisions will have to be made. For example, to manage for birds characteristic of climax communities we will have to allow for stands to exist long past the times of normal harvesting. The Red-cockaded Woodpecker (Dendrocopos borealis) nests in large trees that are usually more than 40 years old. These trees will probably be included less and less in the future in forest management schemes. The present conservation effort is to save nesting and nearby trees. However, if we are regenerating stands at 20-30 years of age, very soon there will be no pine trees of proper age to protect and no woodpeckers. To manage the woodpecker we will have to allow some stands to age past the time of normal harvest. This

may not be easy during a time of high cellulose demand (either on private land or national forest land--at least with the present interpretation of multiple use). The Endangered Species Act calls for the protection of habitat of an endangered species. What does this mean in the case of a Red-cockaded Woodpecker?

Probably the most difficult decisions of all will be to determine management objectives for an area. This will be difficult even if only avian management is being considered. It will be much more difficult when other management objectives are included. Do we want to manage for: (1) the maximum density for some featured species? (2) the maximum number of species for some particular seral stage? (3) a representative avifauna for some biome? or (4) the protection of an endangered species? Will we have small blocks with a lot of edge or large blocks so species that require large areas can be accommodated. How can we justify large acreages of early or late successional stages (usually by-passed in timber management) being reserved for avian or other wildlife management? We cannot accomplish everything with one management plan and tough decisions will be necessary if we really want to maximize avian diversity.

There are many things that we can do to decrease the damage of our current management practices, without greatly affecting our timber production or profits. These all involve the careful selection of the methods of site preparation, planting, maintenance and harvesting plus the manipulation of the size and shape and relative position of each of the even-aged stands. Further flexibility can be attained by providing stands of various successional stages which are not included in the monoculture sere. Frequently this management is very clean with all dead or topped trees removed. This removes habitats for many bird species. Many of the species common in young pine stands are hole-nesting species which depend on dying or dead trees for their nest sites that they construct themselves or for holes made previously by other hole-nesting species. Removal of the dead or dying tree removes these birds as potential breeders. All are primarily insectivores, and would be beneficial to the stands concerned. We are talking about such species as the Downy Woodpecker, Hairy Woodpecker (Dendrocopos villosus), Red-bellied Woodpecker (Centurus carolinus), Carolina Chickadee (Parus carolinensis), Tufted Titmouse (Parus bicolor), Brown-headed Nuthatch (Sitta pusilla), and Eastern Bluebird (Sialia sialis). In England "amenity fringes" of native forests are sometimes left on an edge(s) of a developing stand. This greatly increases faunal

and floral diversity. Another scheme is to plant tolerant hardwoods under fast-growing conifers. The hardwoods will replace the conifers when conifers are harvested (Williamson 1970).

Data are needed on the effects of various silvicultural practices on avian populations. The work of Haapanen (1965) in Finland on coniferous forests is a good example of this type research. Kilgore (1971) showed that reducing the brush and sapling layer by cutting and burning in coniferous forests resulted in small changes in species composition and no change in avian biomass. He said that wildfire or logging would have resulted in greater changes. Emlen (1970) found that burning had a relatively small effect on bird populations in a southern pine forest.

PLANT SUCCESSION AND BIRD POPULATION MANAGEMENT

If the preferred habitat of a game species is known, it is a simple matter, given a free hand with land management, to produce that game species in abundance. Little land is managed exclusively for game, and the game manager more often than not must persuade forester, farmer, stockman, engineer, or bureaucrat to modify his activities on the land to benefit some specific game species or at best some small group of game species.

The same will, and, indeed must hold true for non-game birds. With the exception of areas set aside for the management of the Whooping Crane (Grus americana), California Condor (Gymnogyps californianus), Everglade Kite (Rostrhamus sociabilis), and the Kirtland's Warbler (Dendroica kirtlandii); few acres in this country are devoted exclusively to avian management. Historically non-game birds have benefited or suffered by default from forest management practices. Non-game birds, at least on public lands, will be given more consideration in the future. No longer can the public land manager concern himself entirely with Bobwhites (Colinus virginianus), Turkey (Meleagris gallopavo), Ruffed Grouse (Bonasa umbellus) other game birds and endangered species. Yellow-bellied Sapsuckers (Sphyrapicus varius), Prothonotary Warblers (Protonotaria citrea), Golden-crowned Kinglets (Regulus satrapa) and other non-game species must also be considered.

A mature bottomland hardwood forest in the Mid-South will contain large numbers of Pileated Woodpeckers (Dryocopus pileatus). If the stand is clear-cut the woodpeckers disappear to be replaced by Brown Thrashers (Toxostoma rufum). If the land is reduced to

mineral soil the thrashers leave and are replaced by Water Pipits (Anthus spinoletta); if the site is covered with concrete and skyscrapers and inhabited by 200,000 humans by House Sparrows (Passer domesticus).

Obviously, if we are simultaneously to have Pileated Woodpeckers, Brown Thrashers, Water Pipits, and House Sparrows in relatively large numbers, we must provide four distinct habitats. It becomes more complex when one considers the seral stages of a deciduous forest which, by necessity, grade into each other; the bird communities vary and intergrade even more than the seral stages.

As land managers you must make some hard decisions because your decisions will determine what bird species occur on your land and in what numbers. In most instances you must essentially choose a group of birds (or at best a few groups) and live with them. One cannot manage for "all birds" on a given area any more than one can manage for all game on an area. White-tailed deer (Odocoileus virginianus) management in the Southeast is generally at the expense of gray squirrels (Sciurus carolinensis). Similarly, to manage land exclusively for Pileated Woodpeckers means that Water Pipits will be scarce or absent.

PHYTO-VERTICAL DISTRIBUTION OF BIRDS

The natural geographic range of a bird species is its distribution on the earth. However, birds also have a distribution which is vertical to the earth's surface. Birds show a vertical stratification in vegetation, a situation Dunlavy (1935) termed "phyto-vertical distribution".

That birds show a vertical habitat gradation in vegetation is illustrated by our studies in Louisiana. We found that White-throated Sparrows (Zonotrichia albicollis) spend 75% of their time in a vegetative stratum between the ground and 2 feet above ground. Red-bellied woodpeckers (Centurus carolinus) spent about 75% of the time from 25 feet above ground to the canopy top. The Carolina Wren (Thryothorus ludovicianus) spends 85% of the time in a vegetative stratum above 2 feet from the ground but below 25 feet. We have similar data, based on 4103 observations, for 27 species common to one of our Louisiana study areas (a mature bottomland hardwood forest).

Obviously bird species diversity can be increased in a timber stand if one increases the vegetative strata within the stand. Frequently this can be accomplished by accepting a basal area somewhat less than the optimum

basal area for growing timber alone. The reduced basal area will permit some openings in the canopy and therefore permit vegetative strata to develop beneath the crop trees.

A mature stand of bottomland hardwoods in the Mid-South with a basal area of 150 ft²/acre and a closed canopy will support high populations of woodpeckers (5 species), Blue Jays (Cyanocitta cristata), Carolina Chickadees (Parus carolinensis), and Tufted Titmice (Parus bicolor) but few White-throated Sparrows, Rufous-sided Towhees (Pipilo erythrophthalmus), and wrens. By reducing the basal area to say 115 ft²/acre some ground cover will develop and within a year or so the stand will support not only woodpeckers but also sparrows and towhees. As the openings fill with saplings and young trees the ground cover will persist for some years but now there are three vegetative strata and White-eyed Vireos (Vireo griseus), Yellow-rumped Warbler (Dendroica coronata), etc. will join the previously named birds in the stand.

Succession is still our topic since even the small openings in an otherwise closed or nearly closed canopy are going through the early seral stages and providing habitat for birds with an affinity for that successional stage. Therefore, succession need not imply one seral stage at a given time on a given area and the birds associated with that stage; but it is necessary, if the continuous harvesting of the forest is to occur, to provide several seral stages in one locality and thereby increase both species diversity and bird density for that area.

ENDANGERED SPECIES

The most recent version of the Endangered Species Act (PL93-205) became law on 28 December 1973. It supplants the Endangered Species Acts of 1966 and 1969. All of these laws are designed to prevent, if possible, the extinction of endangered forms.

The new law differs from the previous ones by providing two categories of listing: (1) "endangered" or threatened with extinction and (2) "threatened" or threatened with endangerment. The listing process is now modified so that populations in any geographical area (of significant portion of an animal's range) may be listed. This allows populations to be listed regardless of the status elsewhere.

Section 7 prohibits any federal action that would be detrimental to critical habitat of any listed species. Federal agencies are supposed to utilize their resources to benefit

any endangered or threatened population. Incentives for cooperative programs with states are provided and consequently many states are drafting their own endangered species legislation (Marshall 1975).

Of the 53 avian species currently on the endangered species list, 23 are species of deciduous forests, loosely defined, or their late seral stages. Of these, 16 are from the forested slopes of the Hawaiian mountains and 3 are from Puerto Rico. The four remaining forms are the Bachman's Warbler (Vermivora bachmanii), Kirtland's Warbler, Ivory-billed Woodpecker (Campephilus principalis), and Red-cockaded Woodpecker (U.S. Bureau of Sport Fisheries and Wildlife 1973).

The main threat to the Hawaiian forms are habitat destruction because of clearing of land, timber harvesting or damage to undergrowth by livestock. Some replacement of native vegetation by introduced species and resultant habitat changes have also had an effect. At lower elevations a problem is the spread of diseases into many of the native populations from non-native avian species by introduced vectors (U.S. Bureau of Sport Fisheries and Wildlife 1973, Warner 1968, Wallace 1971). Many of the native Hawaiian species are on the verge of extinction and a maximum effort will be necessary to save them.

Habitat destruction seems to be the main problem in Puerto Rico (U.S. Bureau of Sport Fisheries and Wildlife 1973).

Two of the four continental North American forest forms on the list, the Bachman's Warbler and Ivory-billed Woodpecker, are species which utilize(d) mature or overmature bottomland hardwood forests. This habitat is now very rare and the Ivory-billed Woodpecker is either extinct or virtually so (occasional reports occur, but none of them are completely convincing). The Bachman's Warbler is small and inconspicuous and could be easily missed at low population densities, but there are few recent records of this species and no known current breeding sites. The Endangered Species Act would call for protection of critical habitat of these species if any can be found.

The other two North American forms on the list are characteristic of seral stages in deciduous forest development. The Red-cockaded Woodpecker occurs in open, old age pine woodlands of the Southeast. This habitat is maintained as a disclimax by repeated fires. However, the modern trend in forestry is to harvest pine trees before they reach the desired age for this woodpecker. In addition the required nesting site is a living pine tree with red-heart disease. Another current

trend in forestry is to eliminate these trees. A recent case of the endangered species act of 1973 in action occurred at Fort Polk, Louisiana, when the planned location for new military barracks was changed when a colony of these birds was found.

The Kirtland's Warbler occurs in the northern part of the lower peninsula of Michigan in areas of young jack pine (Pinus banksiana) with low brushy undergrowth. The nesting habitat is a seral stage and thereby ephemeral. However, the forest service has set aside 4,010 acres of National Forest to be managed to provide nesting habitats for this species (U.S. Bureau of Sport Fisheries and Wildlife 1973). This is an example of management to maintain a seral stage necessary for the survival of an endangered avian species. The new Endangered Species Act has the potential of having a profound effect on future activities of man. The extent of this effect will depend on how "critical habitats" are defined and what animal forms are included. As the law reads, a species of grasshopper or an amoeba population is to be protected where that population is listed as endangered.

INFLUENCE OF EXOTIC SPECIES

Avian Species

We have all seen the results of the introduction of some exotic species. Many of these species seem to do well in disturbed habits. Man now is constantly accelerating his rate of disturbance of most natural ecosystems. Often the results are to make the habitat more suitable for introduced species. We are all familiar with the spectacular success of the Pigeon or Rock Dove (Columba livia), European Starling (Sturnus vulgaris), and the House Sparrow (Passer domesticus). These have been in the continental United States for a relatively long time and have out-competed some native forms. Recent introductions have also met with great success. The spread of the Cattle Egret (Bubulcus ibis), which seems to use a previously unexploited North American niche, has been spectacular. The recent spread of the Monk Parakeet (Myiopsitta monachus) has caused much alarm, and there is talk of exterminating this rapidly spreading species.

The area of greatest concern with introduced species in the United States is Hawaii where many species have been introduced. Many of these introduced species have been very successful in out-competing the native-Hawaiian forms--many of which are nearing extinction (U.S. Bureau of Sport Fisheries and

Wildlife 1973, Warner 1968).

The Lacey Act is supposed to control importation, but the pet industry is now very active and accidents may still occur: e.g. Monk Parakeets.

Other Animal Species

Of course, species are introduced other than birds. Some of these will have an effect, either direct or indirect, on bird populations. Some of the domestic animals introduced into Hawaii have caused marked changes in the forest vegetation, for example. These vegetation changes have in turn affected the native avifauna (U.S. Bureau of Sport Fisheries and Wildlife 1973, Warner 1968, Wallace 1971).

Of course the introduction of any form which acts as a predator or competitor may have noticeable effects on avian populations.

Many invertebrates may also have profound direct or indirect effects. In Hawaii, for example, the imported night mosquito (Culex pipiens) has acted as a vector for the spread of diseases such as bird pox and avian malaria (incidentally, the malaria was introduced with some of the exotic birds imported into Hawaii). There are no longer many species of native Hawaiian birds to be found at elevations below about 2000 ft. (even where suitable habitat exists) because of the susceptibility of the local avifauna to disease (mosquitos cannot survive above 2000 ft.) (Warner 1968).

Introduced insects frequently do not have any established means of population regulation in their new environments and soon reach epidemic proportions, often causing much damage to man's crops. Often it seems necessary to counter these outbreaks with application of various chemical insecticides--frequently with harmful side-effects to birds or other elements in the ecosystem.

Others

Certain diseases, of course, are sometimes introduced, and they have their own negative impacts. These probably are never introduced purposefully, however, and man should exercise every precaution to prevent their occurrence.

The chestnut blight is an example of a disease that has had a profound effect on our eastern deciduous forest. It may not have had a great effect on any particular avian species, because bird distribution is

more dependent on plant form than plant species. However, it did change the prevalent seral stages in some areas and thereby affected bird communities.

Introduced plant species also occasionally have noticeable effects on the avifauna. In Hawaii the replacement of native vegetation by introduced exotics has been suggested as another cause of the general environmental deterioration leading to the extinction and reduction of native Hawaiian habitats (U.S. Bureau of Sport Fisheries and Wildlife 1973, Warner 1968).

In Florida the establishment of the Red-whiskered Bulbul (*Pycnonotus jocosus*) has been attributed to the exotic introduced flora of Southern Florida (Carleton and Owre 1975). Other avian exotics are also apparently becoming established in that region. In other words, an entirely new flora and fauna is, or has been, established. To our knowledge the effects of the exotic flora on the native avifauna have not been determined, but we would be surprised if substantial changes in the distribution and abundance of native species has not occurred in Southern Florida.

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Silvicultural Options and Habitat Values in Deciduous Forests¹

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Abstract.--The avifauna diversity provides a challenging and unique opportunity to coordinate timber and wildlife management. Management options should consider three concepts: (1) structural characteristics of the vegetation greatly influence avifauna composition; (2) birds (of different species) occur in nearly every landscape condition; and (3) species differ in their habitat specificity. We have discussed the options of exploitation, even-aged management, uneven-aged management, and preservation. Future silvicultural systems should consider the broad forest perspective, provide for species with specific habitat requirements, and coordinate avifauna inventory with forest inventory.

INTRODUCTION

The key to the value of any "state of the art" publication lies in the ability of the authors to find significant publications and synthesize the data and conclusions into a usable format. Our assignment, covering the great diversity of the deciduous forest ecosystems, at first seemed overwhelmingly broad. We located material on silvicultural practices and articles on nongame bird habitats and population structures. Very few authors have attempted to relate silvicultural options to bird habitat characteristics or *vice versa*. The volumes of silvicultural information are largely concerned with growing high quality trees to a harvestable size in the shortest possible time; economics plays a major role in the application of silviculture.

It is the goal of this article to review and summarize both the silvicultural information and the bird habitat-population data and synthesize the knowledge into a format useful to the forest manager. The actual

impacts of the effects of silvicultural options on bird population characteristics are often speculative as they have not been tested. Many questions are raised requiring research for answers.

We have approached this assignment from a conceptual point of view. Several concepts will be referred to throughout the paper with specific examples given when data are available and applicable. Following is a brief discussion of each of these concepts. First, is the importance of vegetation structure in influencing avifauna composition and diversity. This concept has been discussed in a previous paper given by R. P. Balda. In the deciduous forest ecosystem, six distinct habitat layers can exist. These are bare ground, forest floor duff, herbaceous ground cover, low understory shrubs, midstory, and overstory trees. These layers exist in different combinations. The configuration of one layer, especially the overstory, influences the structure of other layers. Silvicultural practices greatly influence the characteristics of these layers.

The second concept is that of influencing bird species composition by land use practices. The avifauna, composed of approximately 400 species of birds in the area, contains species adapted to nearly every habitat type. For example, the Killdeer ^{3/} will select a bare-ground type, the Yellow-breasted Chat a brushy

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^{3/} Common names from AOU 1957.

area, and the Pileated Woodpecker prefers extensive areas of mature or over-mature woods. Wildlife biologists in the past have been primarily single species oriented, therefore, they discussed the impacts of a given land use practice on the habitat of one species (usually a game species). In the area of non-game bird management, we must recognize that birds will be present in virtually all habitats, but species composition, population density and/or diversity will be influenced by timber management practices.

The third concept is that of adaptability to habitat variability. Bird species vary greatly in the specificity of their habitat requirements. Species that require specific habitat components are referred to as stenoeious--or literally, narrow house. These species require a specific habitat component to complete at least one phase of their life cycle. The Pileated Woodpecker has specific habitat requirements of a mature forest with some dead trees scattered throughout. Some species are quite adaptable to habitat variability--euryoeious. Euryoeious species include the Blue Jay and Cardinal. The stenoeious species provide the greatest potential and challenge for management. Nearly all the endangered and threatened species are stenoeious. Bird species that select specific habitat components can be used as indicator birds, in other words, population and distribution changes in these birds will indicate changes in specific habitat components.

The comments and discussions that follow are meant to apply to portions or all of the eastern deciduous forests (Table 1). These forests cover a big area with a wide variety of vegetation types, topography, climate, soils, and land use patterns. Where information is available examples will be used from each of the major deciduous forest subtypes (USDA, Forest Service 1973).

Table 1.--Deciduous forest types in the United States and primary silvicultural systems (USDA, Forest Service 1973)

Interior Alaska Hardwoods	
10 million acres	
Paperbirch, quaking aspen, balsam poplar, black cottonwood	
Intolerant - fire dependent	
Rocky Mountain Aspen	
6 million acres	
Quaking aspen	
Pioneer species or fire climax	
Intolerant	
Clearcut and/or burn	

Lake States Northern Hardwoods
 10 million acres
 Sugar maple, yellow birch, eastern hemlock, beech, American basswood
 Sugar maple, eastern hemlock, balsam poplar - very tolerant
 Yellow birch - intermediate
 American basswood, paper birch - very tolerant
 All-age selection cutting - veneer - shade tolerant species favored
 Even-age needed for less tolerant species
 Shelterwood cutting for flexibility
 Shelterwood cutting can be used for yellow birch

Lake States Aspen
 13 million acres
 Quaking aspen - very intolerant
 Complete clearcutting best

Oak-hickory
 116 million acres
 More valuable species are intolerant to moderately intolerant
 Clearcut

Northeastern Northern Hardwoods
 15 million acres
 Sugar maple, American Beech, yellow birch, paper birch, white ash
 Selection cutting - recreation - tolerant species favored - sugar maple, beech, hemlock, red spruce
 Even-aged management best silviculturally

Cherry - Maple
 12 million acres
 Second-growth forest on Allegheny Plateau
 Black cherry and white ash - intolerant
 Even-age silviculture - shelterwood best

Appalachian Mixed Hardwoods
 No acre estimate
 Northern red oak - yellow poplar
 Clearcut

Oak - Pine
 27 million acres
 Will go to oak if undisturbed
 For pine - clearcut - burn - herbicide

Oak - Gum - Cypress
 13 million acres (Atlantic Coastal Plain)
 Mixed bottomland hardwoods - clearcut
 20 million acres (Gulf States)

A brief point concerning the usage of the word habitat is appropriate to better understand some statements that follow. Habitat is defined as the natural abode of a plant or animal. Animal ecologists usually

describe the habitat of a species by characteristics such as soil, topography, climate, or vegetation. The habitat description can be subdivided to refer to nesting habitat, feeding habitat, winter habitat and etc. Our usage of the word habitat is organism oriented as above. Another occasional usage of the word habitat or habitat type refers to a unit of land having a narrow range of environmental variation (Deitschman 1973). This usage is inappropriate for our discussion as it is not organism oriented and is subject to arbitrary limits of environmental variation in relation to mapping objectives and any species requirement association is coincidental.

SILVICULTURAL PERSPECTIVES

Historic

With some notable exception the past 40 years have been characterized by an increase in forested acreage over much of the area occupied by deciduous hardwood forests. This has been paralleled by an increase in average stand age, stand-size, and volume as formerly logged areas have become reforested and have matured under fire protection and improved forestry practices. However, some types, for example bottomland hardwood forest, have steadily declined in recent years with drainage and conversion to pasture and row-crops, inundation by reservoirs, and losses to other non-forest uses. There are indications that the trend toward increased acreage may reverse for the upland forest type in response to the world food shortage. This trend reversal is already apparent in the Missouri Ozarks where it is estimated that between 150,000 and 200,000 acres of oak-hickory woodlands have been converted to pasture land annually. The area of commercial forest land in Missouri decreased by 10.5 percent during the period from 1959-1972 (Essex 1974). Monitoring to detect changes in forest resources and related bird populations is desirable.

Economic

Economics play a dominant role in the selection of silvicultural alternatives. Hardwood silviculture in the oak-hickory types, for example, is seldom profitable on sites poorer than oak site index 55. In such cases either pine management or conversion to pasture land generally produce greater economic returns. Conversely, areas with high site index for hardwood on favorable land forms tend to be converted to non-forest uses especially row crops. Thus hardwood silviculture is economical chiefly on moderate

quality sites or land forms unsuited for cultivation. These economic pressures may have an adverse impact on local or regional bird populations or on stenoeconomic species occurring in geographically limited habitat types. These problems will not be solved until we define benefits which justify management for non-economic purposes. Profitable hardwood silviculture, in some areas, may require the production of short rotation roundwood products, such as aspen pulpwood in the Lake States. Potential impacts of short rotation forestry practices on bird habitat values are discussed later.

IMPACTS OF SILVICULTURAL OPTIONS

Options

Silviculture has been defined as: (1) the art of producing and tending a forest; (2) the application of the knowledge of silvics in the culture of a forest; and (3) the theory and practice of controlling forest establishment, composition, and growth (Smith 1962). In the narrow sense silviculture addresses itself to the technical aspects of economical wood production. But in the broad sense silviculture is the care and tending of forests for all the many values which a forest may yield. Thus silvicultural skill may be used to mold the forest in any desired direction and into any form or condition.

We submit that there are four broad management options open to the hardwood forest manager each with its own implications to avian habitat values. These options are exploitation, even-aged management, uneven-aged management and preservation. The exploitation options involves no silvicultural system. The silvicultural systems which might be employed to implement the even-aged management option include shelterwood, seedtree, and clearcutting systems. The selection system, either single tree or group selection would be used in uneven-aged management. The preservation option includes active protection of a stand or the no-management, no-use, leave-alone option. How these options might affect nongame birds are as many and varied as the bird species and forest types involved.

Exploitation

Exploitation of forests is the absence of silviculture; the "cut-out and get-out philosophy". Management focuses on the profitable liquidation of the timber resource without regard to the future yield of forest products or related resources. Depending upon cutting intensity and events subsequent

to logging, the exploited forest normally develops a distinctive two-storied condition of scattered, non-merchantable relics overtopping an even-age understory. Such stands may be small or extremely large -- extending to the boundaries of the property and including numerous pockets of older stems. A large proportion of Eastern National Forests are the result of such treatment and date to the railroad logging era of 40-60 years ago. A landowner who chooses to exploit his timberlands today might expect his forest to be rich in the early successional bird communities in cutover portions and late successional species if any area remains uncut. In the early stages dense shrub cover, as well as abundant nest cavities among the surviving overstory cull stems would prevail. While den cavities and snags might be numerous, other attributes of the climax forest attractive to late successional species would be found wanting.

Even-aged Management

With few exceptions (Marquis 1967), even-aged management (EAM) is recommended by hardwood silviculturists, primarily because other systems fail to produce adequate reproduction and growth of desirable intolerant species (Sander and Clark 1971, Trimble 1970, Arend and Scholz 1969, and Roach and Gingrich 1968). Three silvicultural cutting systems are employed to achieve even-aged stands -- seed-tree, shelterwood, and clearcutting. Stands managed under EAM typically pass through six recognizable stages in a dynamic progression including annual weed, brush, sapling, pole, small sawtimber, and mature sawtimber stages. The two types of operations in the life of an even-aged stand are the harvest cutting and intermediate treatments (thinnings).

Silviculturally the harvest cut has two objectives -- to reap the final crop and to regenerate the stand harvested. Regulation is by area with the acreage of harvest cuts based on rotation -- or the average time required to produce a crop of assumed average diameter. Normally, rotation age for timber production is much less than the pathological maturity of the tree species under management. Recommended rotations range from 30 years for aspen up to 100 years for oak-hickory and bottomland forests. Seed tree cutting is presently not recommended nor needed for hardwoods. Shelterwood cutting with two or more cuts is recommended for some species, i.e. sugar maple, beech, and certain bottomland hardwoods, as much to achieve landscaping and aesthetic objectives as successful stand regeneration. Clearcutting is suitable and recommended for many hardwood forest types.

Under even-aged management, the size and shape of harvest cuts influence horizontal diversity and the amount of edge available between types. The timing and distribution of harvest cuts affects the kinds of edge available and the progression of age classes over the landscape. Vertical diversity within stands is minimized, unless cutting is purposefully modified to achieve multipurpose benefits, but diversity between stands is maximized to the extent that various age classes and forest type are present in the management spectrum.

With hardwoods, regeneration is mainly from natural sources. Following a clearcut, the standard practice is to remove all residual stems greater than two inches in diameter to reduce competition with the oncoming reproduction. This is accomplished by injection of silvicides, cutting, shearing, breaking, and sometimes prescribing fire as in aspen management. Seedbed preparation is seldom necessary since regeneration normally originates from seed stored in the duff or from seedling sprouts. It is probably significant that on the National Forests, cutting either by felling or shearing has essentially replaced herbicides in site preparation. As a result, few if any, stems remain standing to become roost, perch, or den trees unless intentionally reserved.

Hardwood stands are seldom regenerated by planting because suitable techniques are lacking, but research to find successful methods of propagating and planting nursery reared superior hardwood stock is underway. A major problem in artificial regeneration of hardwoods is control of competition with natural regeneration, primarily rapid growing sprouts.

Once the new stand is established, thinning treatments are applied to young and intermediate-aged stands for the purpose of molding species composition, promoting rapid growth and vigor, and salvaging volume which would otherwise be lost to mortality. By accelerating the growth of crop trees, thinnings have the objective of shortening the economic rotation. Presently up to four such treatments are envisioned for managed stands. Where previously unmanaged stands are brought under even-aged management for the first time, a release or removal cut may be applied to remove relics and culls that are suppressing the growth of the featured stand and to mold species composition.

Unless modified by wildlife management constraints, intermediate treatments tend to reduce species variety and overstory density

and to remove the poor vigor or damaged stems most prone to develop cavities. Thinnings promote vertical diversity by stimulating growth of the understory and midstory layers. Rapid crown development and accelerated fruit production of both overstory and understory layers are generally favored with thinning treatments. Understory response following thinning is related to site quality, residual crown density, overstory composition and successional stage of the stand. The impacts of intermediate and harvest cuts on bird populations are variable and not well defined. A few examples of potential impacts on selected bird species are given later in the paper. Much research is needed to define bird-forest cutting interrelationships.

There are some distinct differences in managing hardwoods and pine under the even-aged silvicultural option. Prescribed burning is not usually recommended in the hardwood forest. Fire control permits the accumulation of "duff" which harbors food species for several "forest floor" bird species including the Ovenbird and Woodthrush. On better sites, a dense midstory shrub layer will develop if fires are prevented. Regeneration cuts in deciduous forests usually cover smaller areas than clearcuts in the southern pine forests. The small size of harvest cuts and the better soils lead to the development of a highly diverse community. In deciduous stands, the sun reaches the forest floor all winter which enables certain wildlife food plants, such as vetch in the south, to flourish (Perkins 1972).

The nongame bird habitat management alternatives in the eastern deciduous forest are numerous, but specific objectives of wildlife habitat management plans are often ambiguous or ill-defined. It has been shown that breeding bird density increases with increased development and density of the understory shrub layer (Hooper *et al* 1973). Increasing shrub density by eliminating fire or other techniques, however, will be detrimental to populations of Prothonotary Warbler, Robin, and Red-headed Woodpecker, as these species prefer open park-like forest stands. Adams (1908) discussed the association between plant and bird succession and noted the greatest variety in birdlife in the intermediate stages of forest succession. The decline in species diversity at the climax stages of succession is supported by Karr (1968) in Illinois, and by Bond (1957) in Wisconsin. A general increase in diversity through all stages of succession was reported by Shugart and James (1973) in Arkansas and by Johnston and Odum (1956) in Georgia. Although more research is needed to explain these differences, we do know that many of the old field, brushland,

and forest edge birds do require early successional stages, or early stages of forest stand development.

A careful review of Hooper *et al* (1973), Shugart and James (1973), Kricher (1973), James (1971), Kendeigh (1961), Bond (1957), and Pettingill (1956) reveals the true complexity of population-habitat interactions among the many bird species of the deciduous forest. For generalized nongame bird management, the land manager should strive to achieve and/or maintain a mixture of successional stages and forest age class categories in different size stands. Some stands, especially the mature ones, should be over 80 acres in size. Some bird species seem to select for larger continuous tracts of forest, however, very little specific information is available on species-area relationships.

Specialized management plans could be initiated where one or more species requires "featuring" because of low population numbers, restricted range, or special interest. For example a prescription might call for the control of understory shrub species in a mature forest to create a park-like stand for the Cooper's Hawk, Barred Owl, Prothonotary Warbler, Robin, and Red-headed Woodpecker. Another prescription would be to maintain an old field (with fire) in low growing herbaceous cover to provide habitat for Eastern Meadowlarks, sparrows (several species), and Bobwhites. Other birds that show definite habitat preferences include: those that depend on large trees (Northern Oriole and Hooded Warbler); those that depend on brushland (Common Yellowthroat, Gray Catbird, White-eyed Vireo, and Kentucky Warbler); and the forest edge species (Mockingbird, Yellow Warbler, Yellow-breasted Chat, Indigo Bunting and Blue-winged Warbler).

Uneven-aged Management

For the purposes of this paper uneven-aged and all-aged management are lumped. Harvesting is done at scheduled intervals and the trees to be cut are selected, whether individually (single tree selection) or in small groups (group selection). Selection is made on the basis of apparent age, diameter, vigor, form or species. Non-commercial treatment may follow commercial harvest to remove cull stems and undesirable species. Regulation is by volume and diameter rather than by area. Uneven-aged management tends to favor shade tolerant species and to maintain a climax state or advance plant succession toward the climax community (Filip 1973). Intolerant or midtolerant species may sprout but fail to

develop, thus the selection system is generally not recommended in hardwood silviculture. The possible exception is in the silviculture of northern hardwoods in the Lake States and the Northeast (USDA Forest Service 1973). EAM is preferred on most public lands and industrial forests but many woodland owners practice uneven-aged management or "selection forestry" largely for aesthetic reasons.

Uneven-aged management tends to reduce tree species diversity, and overstory biomass, while increasing the density and biomass of the midstory and shrub understory (depending upon site factors). Thus vertical diversity is enhanced while horizontal diversity decreases. We found no direct information on how these changes will influence bird populations. We can speculate on a few changes in the bird habitat values. The amount of edge habitats would probably decrease within a management unit. Some birds, like the catbird, seem to adjust to small opening (Bond 1957) and may utilize the edges resulting from group selection cutting. Other birds requiring larger openings may not adjust to uneven-aged management options. The non-commercial removal of snags and cull trees may influence cavity nesting species. Here again we lack information on specific comparisons of vertical and horizontal plant diversity.

Preservation

Preservation as a management option has as its objective the development of a natural appearing forest, free from any evidence of logging. Presumably the end result is the eventual development of old growth, if not climax plant community. Preservation is the selected objective of many federal, state and local agencies as well as private organizations and individuals. Like any other form of management, it has certain impacts upon wildlife habitat. Stand structure and composition will vary with climatic and edaphic conditions, overstory density, past use, fire history, wildlife and livestock browsing, and in the case of bottomland hardwoods, flood frequency, timing and duration. Bond (1957), Odum (1950) and others have shown that the diversity of bird species is maximized at the preclimax or middle successional stage and that the number of species as well as total numbers of individuals is less at the climax stage, however, as previously discussed, this is not always true. A group of forest dwelling birds such as the Red-eyed Vireo and the cavity nesting species of woodpeckers and owls would probably benefit from preservation objectives. Fire, storms, and site differences may be effective in creating a mosaic of stands even within a preservation framework.

IMPACTS OF NATURAL PHENOMENA

Very little is known concerning the impacts of insects, disease, fire, drought or storms on avian habitat values. Most studies report only economic damage, or loss, to the timber resource. There is a real need for research to determine the ecological relationships between avian habitat values and natural phenomenon. Ecologically, a natural catastrophe such as a fire, tornado, or severe drought might significantly alter the habitat even if such a phenomenon only occurred once in 100 years. The deciduous forest develops very slowly through many stages before acquiring the characteristics of a mature woodland. Each of these stages are inhabited by different bird species. This diversity of birdlife indicates that all stages of deciduous forest were available throughout bird species evolutionary history.

Insects

Insects are among the most abundant forms of life in the forest. They exert a continuous influence through all stages of forest development. Various attempts have been made to express in monetary values the annual loss attributable to forest insects. Most of these estimates relate to the coniferous forest species such as the southern pine beetle or the spruce budworm. Craighead (1950) estimated the following annual losses caused by forest insects:

Bark beetles	\$ 20,000,000
Defoliators	20,000,000
Insects of forest products	60,000,000
Insects of ornamental trees	<u>100,000,000</u>
Total	\$200,000,000

This loss is probably conservative considering the interrelations between insects and fire and between insects and diseases.

Insects, like other living things, are susceptible to mortality factors that tend to balance population numbers with habitat characteristics. Insect enemies include other insects, bacteria, virus, protozoa, fungus, parasitic nematodes, small mammals, and birds. Many species of birds are insectivorous. Nuthatches, chickadees, creepers, warblers, kinglets, woodpeckers, and many more. Many seed eating birds such as the sparrows and finches become primarily insectivorous during their brood raising activities. Large numbers of insects are consumed by the forest birds; the influence birds have on

insect numbers is reported from specific outbreaks in very limited areas. McKnight (1968) reviewed papers by Mook (1963), Morris *et al* (1958), Dowden *et al* (1953), Mitchell (1952), George and Mitchell (1948), and Kendeigh (1947) and concluded that predation by birds on three species of budworms occurs, but bird effectiveness against high budworm populations appears limited.

Even less information is available on the impacts of insect control programs on bird population levels. Available information is usually quite vague or applicable only to a special case where other factors are involved. NAS-NRC (1962) list several potential hazards of insecticide application to wildlife, but do not discuss specific and quantified impacts of pest control on bird populations. The potential dangers include:

1. Simultaneous treatment of large contiguous areas. Insecticide effectiveness on a diversified area often requires the selection of a broad-spectrum chemical. Many wildlife species do not have the opportunity or mobility to escape to nontreated areas. The rate of repopulation of a large area may be slow.
2. Wildlife susceptibility to insecticides may vary with the season of the year.
3. Food supplies may be eliminated or contaminated. Food consumption in warm-blooded animals is inversely proportionate to their body size. Small insectivorous birds may ingest large amounts of pesticidal chemicals in terms of mg/kg of body weight.
4. Species vary greatly in their tolerance to specific chemicals. Chlorinated hydrocarbons have been shown to adversely affect reproductive success in birds that are at the top of certain food chains, i.e. eagles and herons.

Disease

NAS-NRC (1962) stated that insects kill approximately 2.5 billion cubic feet (71 million cubic meters) of growing stock and saw timber each year in the United States. Another 3.5 billion cubic feet (100 million cubic meters) is estimated to be lost in growth. NAS-NRC (1962) estimate that disease losses in timber, due to reduced growth and mortality, is greater than losses caused by insects.

Although disease losses are considerable, no information was located on the impacts of tree diseases on bird habitats in the deciduous

forest. It is common knowledge that diseased trees often provide cavities for the many species of cavity nesting birds. There has also been much written on the apparent symbiotic relationships between the Red-cockaded Woodpecker and red-heart rot fungus (*Fomes pini*) throughout the southern pine forests (Ligon 1971).

MANAGEMENT APPLICATIONS

Management guides prepared by Forest Service (Region 8) are oriented toward featuring songbirds in areas of intensive recreation use and are formulated to achieve optimum diversity in such areas (Holbrook 1974, and Zeedyk and Hazel 1974). The goal is to attract, for visitor enjoyment, large numbers of species and birds to a relatively compact area. The guides are promulgated on the assumption that the habitat requirements of native species will be satisfied on an extensive or forest-wide basis incidental to the management of game species. Region 9 stresses the diversity concept, assuming that if representative types and age classes are maintained and interspersed on a compartment basis, the needs of native species will be perpetuated (Evans 1974 and Rollens 1973).

Hooper and Crawford (1969) separated woodlands into three categories for non-game bird studies--intensively used wooded areas, urban wooded areas, and extensively used woodlands reflecting the relative interest in birding as a recreational pursuit. They stressed the need for quantitative information in management and suggested an increased need for guidance in managing birds for their ecologic and environmental values.

Subsequently, Hooper *et al* (1973) published recommendations for management of wooded recreation areas to attract breeding birds through understory manipulation. Gill *et al* (1974) suggested practices for increasing human enjoyment of breeding bird populations attracted to intensively managed forest habitats. We suggest that more emphasis should be directed toward developing, with the necessary supporting research, silviculturally oriented bird management alternatives and guidelines:

1. That embrace not merely the forest stand but the compartment and regional perspective.
2. That identify in silvicultural terms, the forest habitat requirement of resident species, both winter and summer.

3. That would recommend silvicultural methods assuring perpetuation of critical breeding and wintering habitats of the forest and forest-edge species.
4. That would normalize breeding population densities by forest type and structure class by regions.
5. That would provide for coordinated monitoring of breeding bird populations simultaneous with forest inventory so as to facilitate the possible correlation of population trends with shifting forest land use pressures and trends. This might be achieved by coordinating the capabilities available to the U. S. Fish and Wildlife Service through the Breeding Bird Survey with the periodic Forest Survey efforts of the Forest Service. This monitoring system should insure that the habitat types necessary to endangered, threatened, and unique species do not diminish through lack of attention.

Mast Production and Utilization

Hard mast is the fruit of heavy seeded trees especially oaks, hickories, beech, and walnut. Martin *et al* (1951) list 37 species of songbirds which consume acorns, 11 that feed upon beechnuts, and 6 that use hickory nuts. None are listed as consumers of walnuts. Competition for mast is keen between some non-game birds, game birds, and mammals. Large quantities of beech and acorns are devoured by roving bands of Bluejays even before seed-fall. Red-bellied and Red-headed Woodpeckers consume the acorns of upland and bottomland species. Grackles consume large quantities from the ground.

Hard mast production is notoriously variable from year to year with characteristically erratic boom-and-bust yields although some species are more consistent mast producers than others. While annual mast crops are essentially unmanageable, mast production capability at the forest compartment and even stand level is dependent upon management alternatives. Techniques available to the forest manager are described in papers by Zeedyk (1973), Evans (1974), and in FSH 2609.23R. The principal techniques include selecting a rotation that optimized mast yields by maintaining a high proportion (40-60 percent) of each compartment in mast bearing age classes retaining key areas for mast production, thinning to improve composition of mast bearing species, thinning to promote vigorous tree growth, retaining mast productive stands on all representative sites,

aspects and elevations, selecting methods favoring successful regeneration of desirable mast producers, and removal of apparent poor producers.

In mountainous regions perpetuation of a mast capability at all elevations and aspects is an important defense against mast failures related to spring frosts. Where prescribed burning of Coastal Plain and Piedmont pine stands is practiced, oak inclusions and the ecotones bordering streambottom hardwoods must be protected from fire or risk the loss of both hard and soft mast species. Conversely experience in the North Central hardwoods indicates that some oak types may be lost to encroaching mesic species unless prescribed burned at regeneration (Arend and Scholz 1969).

In a study of mast production of turkey oaks in Florida, Harlow and Eikum (1963) suggested that per acre mast yields would be relatively unaffected by a heavy thinning that removed up to 50 percent of stocking but retained the best bearers, however the growth response of understory forbs and shrubs was significant. Perhaps this information would prove valuable to managers wishing to enhance shrub density or composition without adversely affecting mast capability. Similar findings in a study of Appalachian mixed oak stands indicate that a few individual stems of northern red and white oaks produced a disproportionately large share of total per acre mast yields (Beck, personal communication).

It is likely that the seeds of light seeded species -- black cherry, sweetgum, sweet birch, the maples -- may be more important than mast to non-game birds. More research into managing these species for seed production is indicated.

Cull Trees and Snags

No literature was found that reported results of studies designed specifically to determine the impacts of silvicultural practices on nesting habitat of cavity nesting birds in the eastern deciduous forest. The suggestions for management listed here are derived from synthesizing data on cavity selection behavior. The suggestions have not been tested as to their effect or potential effect on population levels. Much research is needed before adequate and tested habitat models can be designed.

The most obvious and potentially detrimental impact of any silvicultural program is the removal of culls and snags from the forest stand. These trees are important

for providing cavities, potential cavities, and future cavities. The optimum density of cavities is not known at the present time due to variations in requirements and territory size among the cavity nesting species. Territories of most cavity nesting species are less than 2 ha. (5 acres). Flicker population concentrations have been recorded as high as 19 pair per 40 ha. (100 acres), which would be approximately one pair per 2 ha. (5 acres), (Dennis 1969). A 1971 supplement to the Forest Service Manual for California recommends leaving a minimum of two hard and one soft snag per 2 ha.

Stand development in upland hardwoods is a dynamic process. After a clearcut, the first 10-15 years are referred to as the "brushy" stage when there can be as many as 25,000 stems per hectare (10,000 per acre). By age 20, most of the non-timber species have died or been relegated to a subdominant position in the stand. At age 20, the total number of trees will range from 3,400 to 6,200 per hectare (1,400-2,500 per acre). Without thinning, 90 percent of the trees present at age 20 will die during the next 60 years (Gingrich 1971). These dying and dead trees provide the resource for construction of cavities and feeding by woodpeckers. Normally natural cavities do not become plentiful in a stand until the last quarter of the rotation cycle. Thinning a forest stand selects against subdominant, low-vigor, silviculturally defective and low-quality trees. Silvicultural thinning could potentially reduce the value of the cavity nester's habitat throughout the forest cycle.

Recent research (Shugart et al. 1974 and Perkins 1974) has considered the impacts of silvicultural practices on non-game bird species. However, these studies fail to discuss the availability or potential availability of cavities. Shugart et al. (1974) points up the importance of saplings in the habitat requirements of the Downy Woodpecker for feeding, but does not mention nesting habitat.

Most foresters recommend managing the eastern deciduous forest with an even-age silvicultural plan. The creation of cull-free, young, fast growing timber stands greatly reduces the cavities or the potential for cavities in a stand. Several options are available to the forester. Clearcuts should be kept small and planned so that each management unit (compartment) contain a good diversity of stand age classes. The Wildlife Habitat Management Guide for the National Forests in Missouri (1973) recommended that each compartment contain (for a 100 year

rotation age) 40 percent in sawlog stands, 30 percent in poles, 20 percent in saplings, and 10 percent clearcut (regeneration). Another alternative is to leave trees or clumps of trees standing after each regeneration cut. Twenty-seven cavity nesting species are recognized by the Wildlife Habitat Management Guide for the National Forests in Missouri (1973), most of these have territories of less than 2 hectares. A 5 percent tradeoff in timber growing space would provide for .1 ha clump of trees to be left within each 2 ha of regeneration area (a .25 acre clump per 5 acre area). Additional research would be required to evaluate the clumps in clearcut areas. We cannot rely on adjacent stands to provide cavities as, under intensive management, 60-75 percent of the adjacent stands will be too young to provide adequate natural cavities.

Rotation age has a major influence on the cavity nesting bird species. These birds generally require mature forests for at least part of their life cycle. Short rotation cycles (pulpwood) create young, vigorous, fast growing timber stands with very few natural cavities and dead trees. At least part of each management unit should be scheduled for a long rotation period -- in excess of 100 years throughout the oak-hickory type. The Pileated and Red-bellied Woodpeckers are two examples of birds that require extensive mature forest stands. Barred Owls prefer oak woods that have many dead or dying trees and are relatively free from understory brush as their habitat. These conditions often exist in over-mature stands.

Regeneration cuts, even when all culls and snags are felled, provide several years of good feeding habitat for woodpeckers (Table 2). These birds rely on adjacent stands for nesting cavities. Slash should not be disced, chopped, or burned unless it is absolutely necessary to accomplish regeneration goals. This extra site preparation effort is not generally required in the oak-hickory forest if advanced regeneration is present (Conner and Crawford 1974).

Understory Manipulation

Depending upon objectives, the habitat manager might wish to stimulate, retard or reduce the understory of hardwood stands to satisfy the requirements of non-game species. Various options are available for stimulating understory development (Urbston 1973). At regeneration, the means and intensity of site preparation activities may influence initial species composition. Thinnings in intermediate stands stimulate both herbage production

and fruit yields of understory shrubs. Repeated thinnings or selection cuts enhance the growth of a tolerant midstory, but the midstory may develop at the expense of understory and ground level plants. The extent and direction of understory development varies with forest type, site and the proportion of overstory canopy removed through cuttings.

Table 2.--Percent of 60 hours sampled that woodpeckers were seen, by species and habitat type (Connor and Crawford 1974)

Species:	1- Yr.-Old Clear- cut	5- Yr.-Old Clear- cut	12- Yr.-Old Clear- cut	Mature Area
Downy	21	1	4	11
Hairy	31	5	1	6
Pileated	1	7	3	10
Flicker	2	30	1	0
Total	55	43	9	27

While many species of songbirds exhibit a positive response to the diversity in stand structure resulting from understory release, some species require an open or park-like overstory with a clean forest floor or sparse midstory. This may be difficult to achieve in hardwood stands. It may be possible to retard understory development by not thinning or by making only light cuts that remove little overstory canopy. However, the goal of even-aged management is to enhance crop tree growth and vigor through thinnings. These thinnings may be heavy but normally are moderate, thus, not reducing the residual stand below the point of full site utilization. In some heavy thinning situations a real problem of understory control may evolve. Unlike pine silviculture, burning is not a favorable option for understory control in hardwood stands. Neither does livestock grazing nor even overbrowsing by wildlife seem to offer a practical solution. Direct control through severance, lopping, or herbicides may be necessary to create or preserve suitable habitat for specialized species.

Nuisance Bird Control

In contrast to managing forests to promote and enhance non-game birds, it sometimes becomes necessary to control populations

of nuisance species through silvicultural applications. Harke (personal communication) recommended heavy thinning of wintering black-bird roosts to break up and disperse roosting populations of Common Grackles, Red-winged Blackbirds, Rusty Blackbirds, and Starlings. Thinning to 50 percent of normal stocking can be effective, especially if applied soon after a new roost is colonized. Unfortunately the dispossessed birds merely select another stand. Roost control may be necessary to reduce crop depredations as well as acorn mast depredations by grackles.

The Yellow-bellied Sapsucker, can be a menace to commercial timber, shade trees, and orchards. Rushmore (1969) lists 51 species of hardwoods and conifers damaged by this bird in the northeast alone. Damages ranged from ringshake, to staining, decay and even mortality of the trees attacked. Favorite species included hemlock, paper birch, red maple, northern red oak in Maine, and to the South, yellow poplar is favored. No feasible method of silvicultural control was offered. Kilham (1964) reported that Yellow-bellied Sapsuckers prefer to attack trees that have been previously wounded. A possible management application would be to wound non-commercial trees in hopes of influencing feeding behavior.

SUMMARY

The diversity of nongame birds provides a challenging and unique opportunity to coordinate timber and wildlife habitat management plans. In most cases, specific details of optimum plans have not been determined. Management options should be designed with three concepts in mind. First, the structural characteristics of the vegetation greatly influences avifauna composition. Non-commercial tree species may provide the desired structural characteristics. Maximum bird species diversity will exist in management units containing maximum vertical and horizontal diversity of the cover. Second, there are bird species adapted to nearly every habitat type. A land-use practice, from a total nongame point-of-view, does not "destroy" the habitat but may drastically alter species composition. Selected management options should specify which bird species will benefit and which species will be harmed. Third, bird species differ in their ability to adapt to habitat variability. Some species are quite adaptable to changes in vegetation composition and structure and are not dependent on specific habitat component characteristics. Other species have specific requirements and may require greater management consideration.

We have discussed four broad management options open to the hardwood forest manager. These options are exploitation, even-aged management, uneven-aged management, and preservation. Each of these options has different impacts on avian habitat values. Exploitation during the railroad logging era created stands that are essentially even-aged but contain varying amounts of cull trees in the overstory. Most of these stands are currently listed as pole stands with a cull overstory and seem to be well adapted to the cavity nesting forest species. Even-aged management is recommended by most hardwood silviculturists. We have discussed the opportunities for horizontal diversity and an abundance of edge with properly designed regeneration cuts that will maintain a good distribution of age classes. Much research is needed to evaluate different even-aged management techniques from a bird habitat aspect. Too little is known concerning species-area relationships of most bird species to make specific recommendations as to size of clearcuts. Special consideration should be given to the many cavity nesting species, especially where short rotation cycles are proposed. Uneven-aged or selection forestry management practices provide an opportunity for maximum vertical diversity but may limit species requiring early plant successional stages and edges. Forest preservation, over a long period, would favor the late stage succession birds such as the Barred Owl, Pileated Woodpecker, Hooded Warbler, and Red-eyed Vireo.

The highly variable and diverse eastern deciduous forests provide the necessary habitat components for approximately 400 species of birds. We suggest that silvicultural systems of the future be designed to consider the broad forest perspective but be specific enough to identify the habitat requirements of resident bird species. We also suggest that a monitoring system be designed to correlate bird population trends with land-use practices. This system should insure that habitat types necessary to endangered, threatened, and unique species do not diminish through lack of attention.

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Water Management Practices and Their Effect on Nongame Bird Habitat Values in a Deciduous Forest Community¹

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Abstract.--In the future, demands on water resources will play a much larger role in the management of eastern forests. The techniques utilized to manage forest lands for increased water yield and quality will modify existing forest ecosystems. Consequences of these modifications on nongame birds is largely unknown. A synthesis of available information concerning the effects of water management practices on nongame birds is presented.

INTRODUCTION

Songbirds have always added quality to man's outdoor experiences and their importance as a recreation resource has been documented. In 1970 birdwatching and photography accounted for 449,199,000 recreation use-days nationwide (U. S. Fish and Wildlife Service, 1970). In 1971 all or part of 242,000,000 days were spent enjoying recreational birding activities in the Southeastern States alone; benefits assigned to these activities exceed \$7 billion or about 30 percent of the total value of all wildlife-related recreation in the region (U. S. Forest Service, 1974).

Many Federal, state, and local land management agencies are beginning investigations into the recreational value of birds, their habitat requirements, and the effect of resource management activities on their populations. Such information is necessary for the forest manager to coordinate wildlife, timber, and forest management practices (Webb, 1973). No one has really succeeded in defining the recreational and aesthetic value of forest songbirds in tangible terms and consequently, they cannot be quantitatively compared with timber, forage, or water values. The result has been a lack of emphasis on songbird management in multiple-use planning and implementation (Webb, 1973). Unfortunately, there is also a lack of factual information concerning the effects of land and water management on bird populations, especially for forest-dwelling species.

This paper will examine available information concerning the effect of various water management practices on nongame birds. Documented studies and examples will be cited to illustrate the effect of forest management for water quality and yield on bird habitats and populations with special emphasis placed on watershed management.

Most eastern surface water is streamflow from forested watersheds. Increasing urban water demands necessitates that these sites, particularly municipal watersheds, be managed to increase water production and improve quality. In 1973 the National Water Commission recommended that: "The Congress and the President should direct Federal agencies having land management responsibilities to give adequate consideration to water yield as an objective of multiobjective land management plans." (National Water Commission, 1973). However, the public also expects wildlife, recreational experiences, and timber from these same watersheds (Sopper and Corbett, 1973).

INTERRELATED NATURE OF WATER, WILDLIFE, AND FOREST RESOURCES

The temperate deciduous forest in the Eastern United States is a complex of aquatic and terrestrial ecosystems collectively covering about one-third of the country and supporting two-thirds of this nation's people. It has long been thought that the Eastern United States has a surplus of water with no serious foreseeable shortages. However, Douglas (1974) predicts that demands will exceed supply in most parts of the South within 50 years. If this prediction is valid, concern for water yield as well as quality must be included in land-use and multiple-objective planning to ensure sufficient water for municipalities and industries.

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Subsurface flow from deciduous uplands can be substantially increased through forest cover modification. Forest cover removal reduces evapotranspiration losses and thereby increases water yield. Such water yield increases can usually be achieved with little water quality impairment. Specific recommendations for forest cutting and other more intensive forms of vegetal cover manipulation to increase streamflow and reservoir supply are now in use in some local situations in the Eastern United States. This management significantly affects vegetation structure and hence forest bird populations. Watershed managers, to obtain a balanced use of resources, should consider the adverse or beneficial consequences for songbird and other wildlife populations.

HABITAT PREFERENCE OF BIRDS

Birds are affected by land-use changes or treatments that alter the structure of vegetation. In selecting habitat, different bird species respond to different, often subtle, aspects of the vegetative cover. For example, the composition and structure of the upper canopy may exert the greatest influence for some species, while other birds may select nesting and foraging areas on the basis of the understory, size of branches and twigs, extent of ground cover, or the intermingling of several of these aspects (Cox and Blake, 1974 and Wiens, 1969). Several investigators (Lack, 1933; Svardson, 1949; and Hildén, 1965) have suggested that birds select habitat on the basis of "sign stimuli" reflecting availability of food, protection, and nesting sites. As early as 1941, Pitelka reported on the importance of vegetal structure, suggesting that a plant's life form is usually more important to birds than its species. Tramer (1968), in North Carolina, felt that bird species diversity was controlled by several factors, the most important being altitude, physical structure of the vegetation, and direction of slope (which in turn affects moisture, foliage density, and litter decay rate). Wiens (1969) expressed similar views, stating that birds selected habitat on the basis of vegetation structure, but he felt that such proximate factors as landscape, terrain, and substrate features were also important.

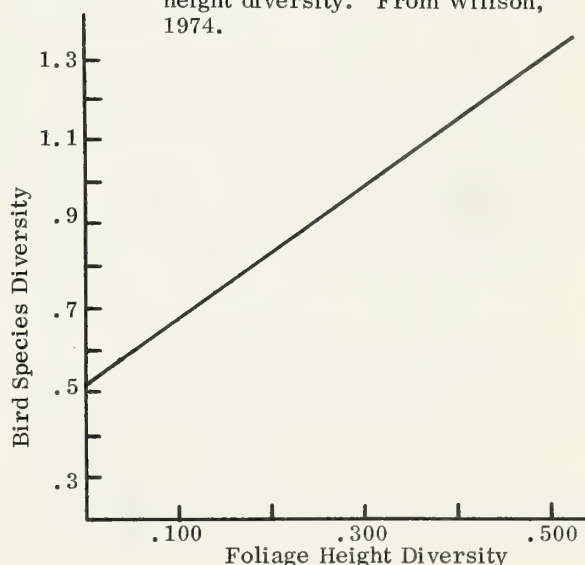
MacArthur and MacArthur (1961) found that foliage height profile determined bird diversity. The number of breeding birds was highest when the three horizontal layers corresponding to herbs, shrubs, and trees over 25 feet tall had equal amounts of foliage. Bird diversity in a forest (basically three-layered) can thus be expected to be greater than in a shrubby field (two-layered) that, in turn, would be greater than in a grassland type (one layer).

Following this earlier work, MacArthur, et al. (1962) developed a method for predicting the abundance of various bird species based on vegetation layers (0-2 feet, 2-25 feet, 25 feet). MacArthur

(1964) found, however, that in more complex habitat types, number of layers of vegetation would not totally account for bird diversity. Presumably the presence of nest holes, water, food sources, changes from deciduous to pine forest, and gradients in vegetation densities affected the acceptability of the habitat for many species.

Willson (1974) found bird diversity to be linearly correlated to foliage height diversity (fig. 1), and curvilinearly with total percent vegetative cover. She reasoned that the expansion of the shrub layer and especially the initial addition of trees had a major impact on the addition of bird species. She found that the development of a good ground cover layer resulted in the addition of one or two bird species. Development of a shrub layer may add another one to four species and, when the tree layer begins to develop, approximately 12 species may be added. As the tree layer becomes well developed, two, or sometimes three, species may be added. Willson concluded that the increase in bird species with the addition of shrub and tree layers may not be due to an increase in resource productivity, but rather to increased habitat patchiness in three dimensions, leading to new possibilities of space utilization by birds. James (1971) investigated habitat ordination of breeding birds and found that occurrence of a certain species consistently coincided with certain structural features of the vegetation. Sturman (1968) found canopy volume and upper-story vegetation to be significantly correlated to Chickadee abundance. Recently, Anderson and Shugart (1974a) found that some species were distributed according to specific habitat variables. For example, Downy Woodpecker abundance was highly correlated to the number of saplings in a plot. Distribution of other species (e.g., the Eastern Wood Pewee) was not strongly related to any one variable, but was weakly related to many.

Figure 1. Bird species diversity vs. foliage height diversity. From Willson, 1974.



The primary habitat characteristic controlling bird density and diversity and greatly affected by land management practices is vegetation structure (Gill, *et al.*, 1974). An appreciation of the effects of modification of the forest structure is thus essential for watershed managers to understand forest bird habitat requirements.

Information from these studies is useful in predicting bird abundance in different habitats and invaluable for assessing possible effects of habitat alteration on a species.

BIRD RESPONSE TO HABITAT ALTERATION

The ability to predict and simulate the response of ecological communities to land-use changes and management disturbances is a prerequisite for effective resource planning and reducing adverse environmental effects (Cox and Blake, 1974). Unfortunately, few of the many ecological studies concerning wildlife response to forest disturbances have included nongame birds (Webb, 1973).

Land and water management activities eliminate original forest habitat niches, replacing them with new and often quite dissimilar ones (Hooper, 1967). Habitat alteration affects bird community diversity and the degree of change is often correlated to alteration magnitude (Ambrose, 1973).

Bird species vary widely in their tolerance to forest disturbance. Some bird species tolerate little alteration while others are found only in severely disturbed forest situations (Webb, 1973).

Niche availability for ground-dwelling species varies with herbaceous and shrub vegetation density, which is a function of forest canopy closure. Total loss of canopy eliminates niches for high-foraging species. Likewise, removal of understory reduces habitat diversity and eliminates niches for low-to-mid-level foragers and nesters. Figure 2 illustrates this point by indicating which species of birds may be affected by alteration of various layers or heights of forest vegetation. Only two species, the Carolina Wren and Ovenbird, occupy a narrow vertical layer (< 20 feet). Thus, any brush or understory clearing would reduce habitat for these species. Both are members of a group that are commonly found on the ground and in the shrub vegetation layer. Other species include the Wood Thrush, Kentucky Warbler, and Hooded Warbler. In contrast, 40 feet is the lowest limit of activity for such canopy-foraging species as the Blue-gray Gnatcatcher, Cerulean Warbler, and Pine Warbler (Anderson and Shugart, 1974). Forest canopy removal would reduce the habitat of these three species.

Clearly certain bird species benefit from forest habitat changes while others are unfavorably affected, depending in each case upon the creation

or destruction of the required niche (Stewart and Robbins, 1958). Species-specific management objectives should be considered prior to actual forest management practices.

WATERSHED MANAGEMENT TECHNIQUES

Management for Water Quality and Its Effect on Bird Habitat

A major consideration in any forest management program should be to maintain high water quality during management activities (Hewlett and Douglas, 1969), but how does the land manager maintain water production of desirable quality and yet manage a watershed to achieve an optimum blend of other forest resources?

Forest management is necessary to utilize timber resources and increase water yield (Trimble, *et al.*, 1974), yet harvesting activities can be damaging to water quality (Stone, 1973; Douglas, 1974). Practices designed to guard against watershed abuse and lowering of water quality also affect nongame bird habitat values. These practices include locating access roads, leaving buffer strips of vegetation between streams and areas of disturbance, and daylighting forest roads.

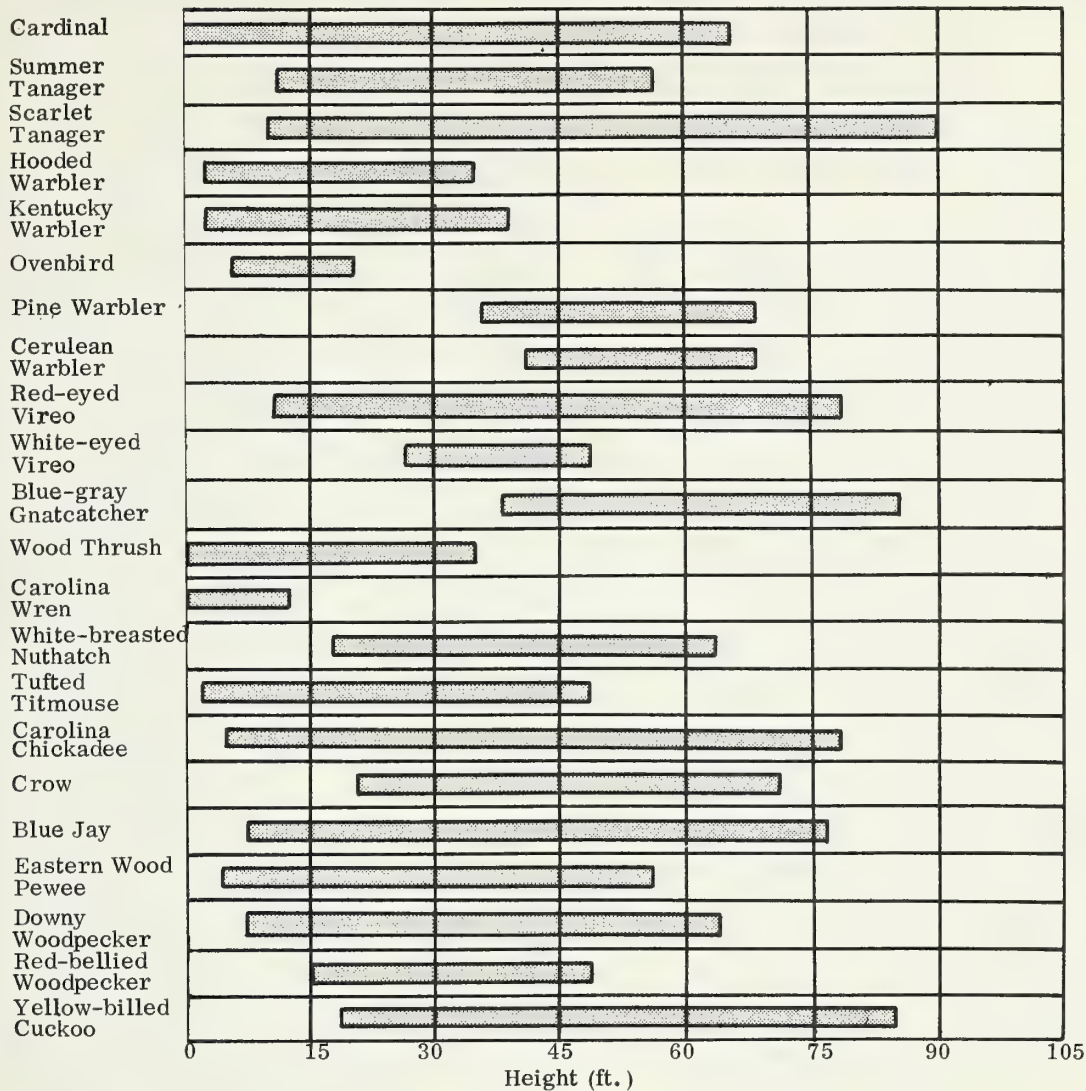
Road Location and Use

One obvious key to effective watershed management is well planned access. Great emphasis should be placed on location, design, and construction of a road system that will require minimum maintenance, meet the current and future area needs, and protect water resources (Douglas, 1967; Kochenderfer, 1970). Many access roads, originally designated as temporary, are used indefinitely for forest management, recreation, and wildlife management. Such unplanned road use can be disastrous to water quality because of washouts and erosion.

The location of forest roads in poorly drained, low-lying, or wet areas should be avoided since these areas become trough-like and hard to drain with heavy use (Douglas, 1974; Kochenderfer, 1970). Soils along streams with perched water tables are particularly susceptible to porosity and permeability reduction through compaction. Unfortunately, bottom lands, flood plains, and alluvial areas are frequently attractive road sites because of low initial construction cost.

Plant communities in these moist low-lying areas usually provide rich wildlife habitat. Odum (1950) states that moist, fertile areas consistently show higher bird densities than more xeric sites and Gill, *et al.*, (1974) observes that moist areas are usually quite productive of birdlife, serving as primary activity centers. Mesic vegetation types supply more diverse foliage strata and greater number of niches for nesting birds (Fawver, 1950;

Figure 2. Height variation in habitat selection of major breeding bird species on Walker Branch Watershed, Oak Ridge, Tennessee. After Anderson and Shugart, 1974a.



Tramer, 1968). The apparent relationship of high breeding bird density to moisture probably indirectly reflects this situation.

For example, Hooper (1967) found 44 percent more breedingbirds and 33 percent more individual species on bottom slope transects as compared to mid-slope transects and attributed this to the richer vegetation on bottom slope sites. The U. S. Forest Service (1974), recognizing the importance of mesic sites to wildlife, has recommended in their Wildlife Management Handbook that wet bottom lands and moist areas be retained for habitat diversity.

Vegetative Buffer Strips

Road systems should be located as far from

streams as possible, both to retain premium habitat and quality water. However, poor planning frequently causes direct disturbance of stream channels. Fortunately, abusive operations that cause streamside damage are being prohibited by timber sale contract provisions on state lands and, in some cases, by forest practice laws that apply to both state and privately owned lands (Stone, 1973).

Recent research has shown that a buffer or filter strip of forest vegetation should be left between harvest operations or roads, and streams. Such strips maintain suitable water temperatures for aquatic life and also reduce impairment of water quality, while preserving stream channel integrity and associated riparian vegetation (Köchen-derfer, 1970).

Filter strips bordering tributaries in flat terrain should be at least 25 feet wide and increase approximately two feet in width for each 1 percent of slope (Trimble, 1959). On municipal watersheds, where water quality is of paramount importance, the size of the filter strip should be increased. Trimble and Sartz (1957) suggest doubling the 25-foot recommendation; thus, the minimum width should be 50 feet with an increase of four feet for each 1 percent of slope.

As with other types of moist sites, riparian zones are frequently excellent songbird habitat and are often inhabited by species with specific habitat requirements. For example, Ambrose (1975), in his study on an east Tennessee watershed, always found the Acadian Flycatcher associated with moist ravines and drainages below elevations that presumably lacked a sufficiently high moisture content. Others have also reported finding this bird mostly along streams in cove hardwood forests (Tramer, 1968; Chapman, 1966). Other species that prefer moist streamside sites include the Louisiana Waterthrush, Prothonotary Warbler, Alder Flycatcher, and Swainson's Warbler.

Whether or not forest filter strips are large enough to accommodate a bird's breeding territory is unknown since little is known concerning the minimum size area required for most species. Although some birds forage over a wide territory, most restrict their breeding activity to an area 1/2-acre in size or less (Gill, *et al.*, 1974). This should, however, be considered only as a generalization. Territory sizes and shapes vary with vegetation structure, population density, richness of habitat, food resources, bird species, and other undetermined factors. Much research work is needed before species-specific territory sizes or shapes and their relationship to habitat conditions can be discussed with confidence.

Ambrose (per comm.) has suggested that species commonly establishing their niche along streams or waterways may be able to adapt their territory both in shape and size to take advantage of the uncut filter strip. In richer habitats the size of a species' territory tends to be smaller. Yet, if the strip is too narrow, there is the possibility of excluding some species whose minimum requirements cannot be met. Filter strips may benefit some bird species by creating small-scale habitat interspersions and edge effect. Ecotones between two habitats generally have higher and more diverse faunal populations than does either habitat alone (Dasmann, 1964; Odum, 1959; Ambrose, 1975). Riparian filter strips usually have maximum edge conditions because of inherent stream sinuosity; however, this edge effect can be further enhanced by feathering or intentional edge undulation.

Daylighting Forest Roads

Another important aspect of water quality control is minimization of traffic on forest access roads during unfavorable weather. It is impossible to control erosion if unsurfaced roads are used during excessively wet weather (Kochenderfer, 1970). However, daylighting (cutting trees and other vegetation along road borders) can be used to hasten drying.

Daylighting exposes wet roads to sun and wind, speeds drying, and reduces maintenance requirements. This practice is especially beneficial along main access roads heavily used by forest recreationists. Daylighting also provides bird habitat diversity through creation of edge and low profile shrub vegetation.

Hooper (1967) in the late summer period (July to September), found 42 percent more birds and 34 percent more species in brushy, cut-over areas than in uncut forest stands. He recommended daylighting as a practice to create brushy areas for birds during this season. Ambrose (1972) studied the effects of daylighting and recorded a dramatic decrease in most forest birds, coincident with an increase in species and numbers of birds associated with edge habitat, woodland clearings, and brushy areas (Table 1). Ambrose suggested that an overhead canopy maintains the "woodland" character of the bird communities along forest roads. However, daylighting increases the suitability of roadside habitat for a large number of colorful and conspicuous "edge" species.

Management for Water Yield

Steadily increasing demands on water resources for residential, agricultural, and industrial needs have stimulated a search for additional water sources. Expanding metropolitan areas have a particularly acute need for additional water supplies (Lull and Reinhart, 1967). Management techniques used to increase yield include various forms of vegetation manipulation, and since a songbird population is tied closely to vegetal structure of a forest community, modifications of forest cover to affect water yield may substantially alter local bird population density and diversity.

Hibbert (1967) reviewed 39 experiments and indicated that vegetation manipulation can have substantial influence on water yield. Hornbeck, *et al.* (1970) determined that water yield could be increased as much as 13.5 inches, or 40 percent annually, by total forest removal. Manipulating vegetation to increase water yields may eventually change the whole nature of eastern forest management (Hewlett, 1966; Lull and Reinhart, 1967; and Corbett, 1969).

However, we should strive to increase water yield in a manner that retains other quality environmental values, including aesthetic, wildlife, and recreational amenities. To achieve this, managers

Table 1. Effect on Songbird Populations of Daylighting a Forest Road

Species	Column A	Column B		Column C
	Total Birds 66-69 Forest Rd. - Closed Canopy	Total Birds 70-72 Forest Rd. - Daylighted		Percent Change
Turkey Vulture	3	1		-66
Broad-winged Hawk	2	2	0	0
Bobwhite	5	17		+240
Mourning Dove	5	4		-20
Yellow-billed Cuckoo	8	8		0
Chimney Swift	2	4		+100
Ruby-throated Hummingbird	-	1		-
Yellow-shafted Flicker	1	-		-100
Pileated Woodpecker	5	3		-40
Red-bellied Woodpecker	2	11		+450
Hairy Woodpecker	2	-		-100
Downy Woodpecker	2	6		+200
Great Crested Flycatcher	8	16		+100
Eastern Phoebe	-	1		-
Acadian Flycatcher	1	1		0
Eastern Wood Pewee	1	3		+200
Blue Jay	9	20		+122
Common Crow	5	2		-60
Carolina Chickadee	19	17		-11
Tufted Titmouse	28	20		-29
White-breasted Nuthatch	2	1		-50
Carolina Wren	5	6		+20
Mockingbird	1	-		-100
Wood Thrush	26	9		-65
Eastern Bluebird	-	2		-
Blue-gray Gnatcatcher	-	5		-
White-eyed Vireo	2	-		-100
Yellow-throated Vireo	2	1		-50
Red-eyed Vireo	35	18		-49
Black and White Warbler	8	1		-88
Black-throated Green Warbler	22	10		-55
Pine Warbler	8	21		+163
Prairie Warbler	2	2		0
Ovenbird	31	14		-55
Louisiana Waterthrush	4	-		-100
Kentucky Warbler	1	1		0
Yellow-breasted Chat	2	1		-50
Scarlet Tanager	6	8		+33
Summer Tanager	8	18		+125
Cardinal	13	9		-31
Blue Grosbeak	-	2		-
Indigo Bunting	8	14		+75
Rufous-sided Towhee	8	10		+25
Brown-headed Cowbird	6	4		-33

Data from Ambrose (1972). Note: Column A - Total number of birds contacted 1966-69 with the actual figure divided by 1.33 to make it comparable with three-year sightings in Column B.

must be able to predict the ecological consequences of their resource management activities.

The magnitude of water yield increase depends largely on the type of forest management employed. Normally, water yield increases directly with the amount of basal area removed, and consequently even-aged management has a greater effect on the magnitude of water yield than uneven-aged management. Clearcutting on a northeast deciduous forest watershed can be expected to increase annual water yield the first year by about 4 to 12 inches, but light thinnings rarely reflect any change in streamflow (Lull and Reinhart, 1967). These increases rapidly decline each year after cutting and within 10 to 15 years, water yield will return to pretreatment levels. Therefore, to maintain a sustained water yield, new areas must be cut periodically as earlier cuts mature.

Effects of Clearcutting

Several investigators have studied the effects of clearcutting on bird populations. Without reference to species, Krull (1963) concluded that clearcutting was detrimental to bird populations in New York State. However, this statement was made regarding the suitability of early growth stages of regeneration for endemic forest species. Hooper (1967) studied an area of southwestern Virginia and found more species and greater bird numbers in the cutover stands. He concluded that clearcutting apparently produced more niches for breeding birds than were previously available. Birds such as the Prairie Warbler and Yellow-breasted Chat, found only on cut areas, are usually associated with early successional vegetation. Hooper also detected a distinct seasonal shift in use of cut and uncut stands. The relative value of cut stands was high during the breeding and late summer period, while more birds were observed in the uncut stands during winter months. Results of Ambrose (1975), who studied small forest clearcuts in Tennessee, agree with those of Hooper. Ambrose (1975) also compared the diversity of the bird populations found on cut areas to that found in uncut forest areas. In general, bird populations tend toward higher levels of diversity as ecological succession progresses (Johnson and Odum, 1956; Kricher, 1973). However, Ambrose consistently found higher bird diversity in the clearcut plots than in uncut forest plots, and attributed this to the interdigitation of grasses, shrubs, and young trees on the cut areas that created habitat niches not found on the uncut forest.

Conner, et al. (1975) investigated woodpecker nesting habitat in southwestern Virginia and found that, of the four species of Woodpecker studied (Hairy, Downy, Pileated, and Flicker), only the Common Flicker readily used clearcut areas for nesting. However, in studies of woodpecker foraging behavior in Appalachian clearcuts, Conner and Crawford (1974) found that Downy and Hairy

Woodpeckers fed on insects located under the bark of one-year-old logging debris. They also found Flickers feeding on ants and fruits on the ground in clearcut areas. Hooper (1967) also observed Hairy and Downy Woodpeckers foraging in dead snags in cutover areas and speculated that the abundance of these birds is not affected by cutting as long as adjacent forest areas remain undisturbed. Thus, these birds require uncut forests for nesting, but utilize disturbed sites for foraging activities.

Conner (1975) studied Bluebirds nesting in clearcuts and found that clearcutting can create acceptable nesting habitat for at least 12 years following timber harvest if dead snags are left standing.

Resler (1972) states that clearcutting undoubtedly provides more diverse habitat for a greater number of species due to the edge effect created by this process. The importance of forest edge to bird populations has been discussed by many authors (Lay, 1938; Beecher, 1942; Preston and Norris, 1947; Brewer, 1958; and Johnson and Odum, 1956). An edge species may be defined as one that requires two or more communities of widely different ecological ages intermixed for breeding territory (Johnson and Odum, 1956). The forest edge community frequently contains many of the bird species of each of the adjacent communities—forest and clearcut—and, in addition, birds that are characteristic of, and often restricted to, the edge habitat. Often, both the diversity of species and density of some are greater in the edge than in either community flanking it (Odum, 1959).

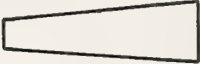

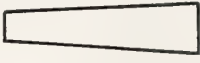
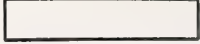
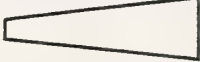
Lay (1938) revealed that the margins of clearings had 95 percent more birds, representing 41 percent more species, than comparable interior areas of adjacent woodlands. Preston and Norris (1947) stressed that the total area of a particular type of vegetation is not as important as the amount and variety of edge present. Gill, et al. (1974) explained, based upon the conclusions drawn by MacArthur, et al. (1962) regarding the importance of vegetal height profiles and habitat patchiness, that an edge habitat derives its importance from the vegetative heterogeneity that provides a greater variety of habitat niches.

Ambrose (1975) computed utilization indexes for 23 bird species, based on frequency of occurrence in one of three habitat types—forest, edge, and clearcut. The Wood Thrush, found in the forest, was the only species restricted to one habitat type. Thirteen species were found in two habitats, while nine were found in all three. Of the 23 species recorded, 22 were recorded within the edge. Table 2 indicates the degree to which these species vary in their habitat preference. Ambrose concluded that populations of the edge are markedly different from the species and numbers of birds in the interior of either the forest or the clearcuts.

Table 2. Representation of the degree of habitat preference by birds in a deciduous forest,
Norris, Tennessee. 1974



Table 2. Representation of the degree of habitat preference by birds in a deciduous forest, Norris, Tennessee. 1974 (continued)

Species	Forest	Edge	Clearcut
Summer Tanager			
Cardinal			
Indigo Bunting			
American Goldfinch			
Rufous-sided Towhee			

Data from Ambrose (1975).

A new clearcutting method, strip cutting, has a profound effect on the amount of edge habitat. Timber is cut in 80-foot-wide strips and the method has been investigated recently at Hubbard Brook Experimental Forest, New Hampshire, as a means of increasing water yield (Hornbeck, *et al.*, 1974). Although water yield is small compared to clear-cutting in blocks, strip cutting gives a tremendous increase in proportion of edge to cutover area and should favor an increase in birds associated with edge habitats.

Effect of Selection Cutting

In 1958-59 three experimental watersheds in West Virginia were partially cut using all-age management practices. Basal area removed was 36 percent, 25 percent, and 14 percent respectively with corresponding water yield increases of 10 percent, 2.4 percent, and 1.3 percent, compared with a 20-percent increase in annual water yield from a commercial clearcut on the same area. All-aged management that involves harvesting of mature trees by selection will have a much smaller effect on water yield than clearcutting (Lull and Reinhart, 1967). The effect of stand thinning on water yield is similar to that of selection cutting. Even with such small increases in water yield, some municipal watersheds are integrating thinning operations with other vegetation treatments to increase yield (Mrazik, *et al.*, 1974; Spencer, 1974; and Heagy, 1973).

Tramer (1968) investigated the effect of forest thinning on birds on experimental watersheds at the Coweeta Hydrologic Laboratory in North Carolina. Tramer (1968) summarized his findings at Coweeta: "Thinning of forests to provide deer browse, remove unproductive trees, or to increase water yield also increases the diversity of the bird population by increasing the physical heterogeneity of the habitat."

Hooper (1967) concluded that thinning of canopy

trees should increase breeding bird density through stimulation of understory growth. Both Hooper (1967) and Gill, *et al.* (1974) recommend that thinning the overstory to achieve a canopy closure of 50 percent to 75 percent would favor songbirds.

Effect of Understory Removal

Removal of understory vegetation, a proposed technique of increasing water yield, has been employed through herbicide usage on some municipal watersheds (Mrazik, *et al.*, 1974). Johnson and Kovner (1956) concluded that, where water needs were critical, specialized removal of forest understory vegetation may provide worthwhile gains. However, the consequences for bird populations would be disastrous.

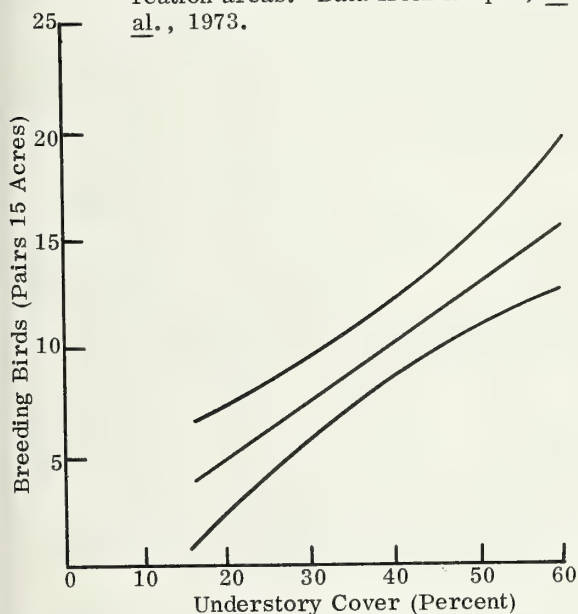
Brooks (1943) reported that the exceptional diversity and abundance of birds in the Southern Appalachians was a result of the rich and varied shrub understory. Odum (1950) studied the Highland Plateau of North Carolina and compared his bird population density to results of Kendeigh (1945), who worked on the Helderberg Plateau of New York. Both areas are in the Appalachian region, but Odum found his area to have nearly twice as many birds as Kendeigh's area. This difference was attributed to higher rainfall and greater development and diversity in the forest understory in the southern region. Dambach (1944), in Ohio, found breeding birds four times as abundant in ungrazed woods with understory as in woods where understory has been removed by grazing.

Preston and Norris (1947) reported that, in an undisturbed woodland, 50 percent of all bird nests were no more than three feet off the ground, while less than 30 percent were higher than six feet. Burr and Jones (1968) concluded that removal of shrubs and understory reduces bird species diversity and nest site availability and forces a change

in nesting habits of some species.

An extremely high breeding bird population of 800 pairs per 100 acres was reported by Johnson (1970) at University of Virginia Biological Station. This was attributed to extensive artificial plantings of laurel and rhododendron shrub understory around the station grounds. Gill, *et al.* (1974) and Hooper, *et al.* (1973) stress the importance of maintaining a moderate-to-dense understory among almost all stages of forest growth (fig. 3). Analysis by Anderson and Shugart (1974a) indicates that understory removal would reduce habitat for such shrub-foraging species as the Wood Thrush, Kentucky Warbler, Hooded Warbler, and Carolina Wren.

Figure 3. Regression of number of breeding birds on understory cover in forestlike recreation areas. Data from Hooper, *et al.*, 1973.



Extensive deadening or removal of both understory and overstory vegetation has been used along watershed riparian zones to increase water yield. Removal of riparian vegetation, even in drought period, will effectively increase water supplies (Lull and Reinhart, 1967; Hewlett, 1966). This practice is currently being employed on watersheds in several eastern states, including Maryland, Massachusetts, New Jersey, and Pennsylvania.

The importance to birds of rich and diverse riparian foliage has already been discussed and extensive removal of this vegetation may completely eliminate habitat from a particular watershed for such species as the Louisiana Waterthrush and Prothonotary Warbler.

Effect of Vegetal-type Conversion

Forest regrowth after clearcutting can lower

water yield increases by two-thirds within five years and reduce it completely in 10 years (Lull and Reinhart, 1967; and Reinhart and Lull, 1965). Thus, to maintain high water yields, watershed vegetation must be converted to a less water demanding nonforest type, either by frequent recutting or herbicide treatment. This practice eliminates timber production and drastically alters songbird habitat. However, aesthetic, recreational, and wildlife values may be accommodated if a cover of shrubs and brush, maintained by annual or semi-annual recutting or herbicide treatment (Hewlett, 1966), is allowed to develop. At Coweeta Hydrologic Laboratory continual cutting gradually produced a closed cover of vigorous herbaceous and low shrubby growth, and water yield stabilized at approximately 66 percent of the increase experienced during the first year after cutting (Hewlett, 1966).

Creation of a permanent shrub community has a profound effect on forest songbird populations. Shifts in species composition occur, with forest birds such as the Ovenbird and Wood Thrush being replaced by species such as the Yellow-breasted Chat, Chestnut-sided Warbler, Catbird, and Indigo Bunting that are closely associated with early successional shrub stages.

Odum (1950) noted that the shrub-stage communities are well occupied by birds, and that population density decreases as the forest matures (288 breeding pairs per 100 acres in the shrub stage, compared to 222 breeding pairs per 100 acres in the forest stage). Kendeigh (1945) and Karr (1968) also found bird densities to be higher in shrubby seral stages than in climax forest. However, Shugart and James (1973), Johnson and Odum (1956), and Saunders (1936) found an increase in density through progressive successional communities toward climax vegetation.

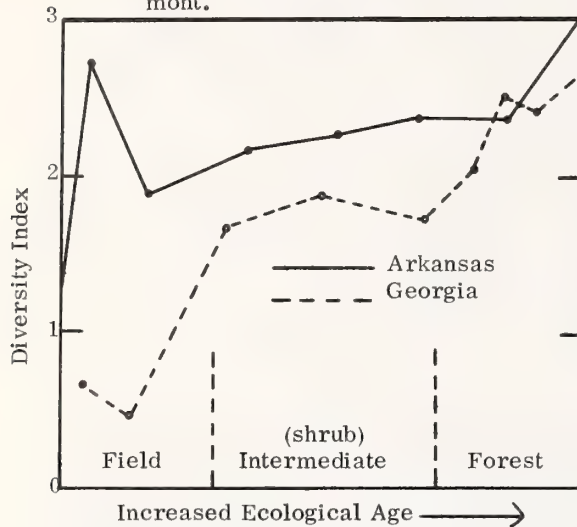
The relationship between bird population diversity and habitat structure has received recent scrutiny by several researchers. Since bird populations tend toward greater species diversity as ecological succession progresses, shrub communities would be expected to have lower bird species diversity than would forest communities (fig. 4).

Several studies indicate this trend: (Shugart and James, 1973; Johnston and Odum, 1956; Kricher, 1973; Karr, 1968). Progressive increases in diversity with ecological age of the vegetation community appear to be a widespread phenomenon, and bird diversity is closely associated with increased foliage height diversity during succession (Tramer, 1969; Karr, 1968; Shugart and James, 1973; MacArthur and MacArthur, 1961; MacArthur, 1964; MacArthur, *et al.*, 1962; and Willson, 1974).

Another method of increasing streamflow is to convert a forested watershed to grass. Such conversion of a watershed in North Carolina increased

annual water yield up to six inches (Hibbert, 1969).

Figure 4. Comparison of bird diversity in the various stages of plant succession in the Arkansas Ozarks and the Georgia Piedmont.



Date from Shugart and James, 1973; and Johnston and Odum, 1956.

Unfortunately, conversion of a forested habitat to a herbaceous field or grass community will substantially alter the existing bird population. Songbird density and diversity are frequently found to be lower in a herbaceous field community than in any other successional stage (Karr, 1968; Shugart and James, 1973; Kendeigh, 1948; Kricher, 1973; and Johnston and Odum, 1956). This is due to the structurally simplistic, two-dimensional nature of the field habitat.

Although fields dominated by grasses and forbs will have a distinctive breeding bird population found in no other successional stage (Shugart and James, 1973), the entire breeding population may consist of no more than four or five species (Kricher, 1973).

SUMMARY AND CONCLUSIONS

In the very near future demands on our water resources will play a much larger role in the management of eastern forests. Pressure for more high-quality water and other forest products may dictate a much more intensive pattern of management. In some areas, the removal and conversion of forest stands to increase water yield will probably be a necessary method of forest management. Many of the water management techniques discussed are already being employed on municipal watersheds in the Northeast.

Concentrated urban populations desire the amenities of open space, natural areas, and related recreational opportunity—bird observation

and enjoyment are important elements. Resource professionals charged with managing municipal watersheds and forested wildlands will be asked to help provide these amenities, in concert with basic water services demanded by urban development in the East.

Land managers should always consider the interaction existing between forests, wildlife, and water resources and be able to anticipate the complex problems in water resource management that include, among other things, the consequences of their activities on songbirds and other wildlife populations. The various techniques utilized to manage forest land for water quality and yield will extensively modify existing forest ecosystems. The consequence of these modifications to songbirds, as well as other wildlife, is largely unknown.

The land manager should attempt to define those features of the vegetation that are altered by various water management practices and simulate the effect these changes have on the ability of a particular watershed unit to provide suitable habitat for songbirds.

There is an urgent need to determine the mix and pattern of forest and water management practices that will produce a desirable combination of water, timber, and wildlife benefits. This need is especially important on municipal watershed lands, quite frequently characterized by multiple use under heavy pressure. Often these areas provide urban dwellers their primary opportunity for outdoor-oriented recreational activities.

There is also a need for a coordinated research program designed to solve our most pertinent problems involving Federal, state, municipal, and private organizations. Management information should be made readily available to those who need it most—the land managers.

In conclusion, the quantitative effects of various water management practices on the songbird habitat values of a treated site are largely unknown. The research approach should involve:

1. Determination of the changes in plant species, abundance, and foliage structure associated with the various water management practices.
2. Determination of the relationship of changes in vegetation to changes in songbird species density and diversity.
3. Development of criteria for the best combination and pattern of forest and water management practices that will sustain desired songbird population as well as meet the primary objective of quality water production.

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Discussion

MR. SWANSON: Mr. Zeedyk, why didn't you include artificial nesting sites as an alternative to the maintenance of snags or cavities for cavity nesting birds?

MR. ZEEDYK: I think primarily our own bias was toward managing the forest in natural ways rather than through artificial direction of nest boxes.

MR. GALE: I have heard that concept proposed before, and to me it takes a pretty narrow view of what a snag is. It only speaks to the smaller cavity nesting birds. A snag is more than just a cavity nest for a bird. It supports the food supply for many birds.

MR. BALDA: Data from southwestern ponderosa pine forests indicate that insectivorous birds spend about ten percent of their time foraging on snags. Snag vital mass is far less than ten percent of the ponderosa pine forests. Thus, snags are being used as a preferred food source. Furthermore, two insectivorous species, the Tree Swallow and Western Bluebird use snags extensively for hawk sites--sites to sit out and look for insects, then fly out and hawk them. Some birds, for example goshawks, use snags extensively for sites to hunt from and also sites to nest in. I think there's a whole range of options here, and a whole range of ideas that we need to consider in terms of snags.

MR. HOMART: I would like to point out, that ambient temperatures inside a nest box are much colder than in natural cavities. Insectivorous birds may freeze in a nest box, but they're probably going to overwinter in a snag.

MR. JAHN: I just want to offer a comment on the importance of knowing the alternatives that are now being considered that will help maintain riparian habitats. In the past we've had structural types of alternatives, whether it be an impoundment through the erection of a dam or whether it be the channelization of the stream in which the riparian habitat is actually removed. In 1974 nonstructural alternatives were authorized in legislation nationally and I think it behooves all people working on individual projects to recognize that that authority now exists, but has not been implemented. So when you come to the matter of a proposal for a structural measure to be placed, such as stream

channelization and removal of the forest vegetation on either side of the stream, consider the fact that non-structural alternatives are available. And I suggest you move forward to push for their implementation. This gives a reasonable alternative that has been fought for for many, many years that should be applied in many situations. The other thing I want to offer a word of caution, and that is when you remove riparian habitat you may--and I say may--increase water yield. But the question is to what degree? The methods by which water yields were actually determined are seriously in question. So don't look at the old literature and assume that those figures are right; they can mislead. Really press for refined data and refined measurement.

MR. DIEM: I'd like to comment on the relationship between number of species of successional stages. First, most avian studies have only been short-term, those are not very well associated in time or space with stages of succession. Second, we have a problem with one of these successional stages in the climax vegetation. In lodgepole pine, there is considerable variation. In some instances it is climax; some cases it is not. The disparity among reports of distribution and density of species indicates that we really don't know enough about successional stages. We think we do. We make broad generalizations, but they have little reality to the community's behavior in nature.

MR. TURNER: Land managers must address themselves to the overgrazing of streamside sites or riparian habitats. We have got to control overgrazing or we are going to lose huge amounts of good habitat.

MR. TOWELL: I have some good news and some bad news. The good news is that I am going to get you out of here promptly at 11:30. The bad news is if you stop asking questions I am going to talk a little. So it's up to you.

MR. WESKE: There has been a lot of discussion here about diversity. The overriding impression is that diversity is good. And this involves perhaps managing for the broadest variety of habitats within a small area. But one must think more in terms of particular species.

MR. TURNER: I'm just wondering if any of the panelists or any of the Forest Service in this

audience know how many ornithologists does the Forest Service employ?

MR. OLSON: I think there's a new concept emerging though in management and the way we go about getting data nowadays. We don't have to have necessarily our own ornithologists. We have the ability to contract with people who do have the expertise. And in this way we really are able to bring in a lot more expertise. And in this way we really are able to bring in a lot more expertise than if we had an expert in every single team that came along.

MR. DIEM: All too many people are ornithologists but not necessarily good ecologists. We have very few people who can bridge the broad gap, integrate what we know, and develop a plan for management.

MR. BALDA: I think there are a number of us in academia who are willing and very, very interested in answering these type of questions. But somewhere along the line we have to be asked. Most of us here are here because we want to be here. We want to help.



Wednesday Afternoon, May 7

Management of Range Habitats

*Presiding: W. D. Hurst
Forest Service, USDA*



Rangeland Avifaunas: Their Composition, Energetics, and Role in the Ecosystem¹

John A. Wiens^{2/} and Melvin I. Dyer^{3/}

Abstract.--We review attributes of breeding bird communities in several types of North American rangeland habitats, emphasizing dominant species, community organization, energy flow and trophic dynamics, and various ways of viewing the importance of bird populations. Rangeland avifaunas are characterized by few breeding bird species; only 20 species occur with moderate frequency in these habitats. The number of breeding species in 10 ha plots averages 3 to 5. Breeding densities average 185 to 329 individuals/km², while standing crop biomass averages 50 to 160 g/ha. There is substantial seasonal and annual variation in density and biomass, but not in species composition of breeding avifaunas. Grazing at high intensity generally reduces species numbers, but has variable effects on densities and biomass; agricultural cultivation produces major changes in all community attributes. In native rangelands, well-defined patterns of avian community structure in species residency, trophic structure, and relative proportions of different sizes of species exist.

Energy flow through breeding avifaunas in rangelands varies from 0.9 to 2.9 kcal m⁻² breeding season⁻¹, but there are few distinctive differences in energy flow between mesic and xeric rangelands. Food consumption is on the order of 0.2 to 0.4 g dry wt m⁻² season⁻¹, with animal prey comprising roughly 80% of the biomass consumed.

INTRODUCTION

Rangeland habitats cover a substantial portion of western North America. Through most of this region, the physical environment is rigorous: Precipitation is generally low and temperatures vary over an annual range often exceeding 100°F (56°C). More important, perhaps, are the longer term irregularities in climatic patterns. Abnormally wet or dry spells occur with sufficient frequency to impose severe stresses on the biota (both native and domestic) of rangelands, and this stress is frequently magnified by interactions among climatic features. Thus a dry year in the prairies not only has

low precipitation, but is accompanied by higher than average temperatures and wind movements and therefore higher evapotranspiration rates. One result is that the need for water in the system may be greatest during the years when it is least available (J. L. Rasmussen, pers. commun.). Further, the occurrence of climatically abnormal years is not only variable but unpredictable (Wiens 1974a), and the effects are often felt over wide areas (Borchert 1950). These general climatic patterns, with thermal and water stresses which are variable in time, impose constraints on vegetational development in rangelands, much in accordance with the precipitation-primary production relationships visualized by Holdridge (1947) and

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Rosenzweig (1968). The vegetation is thus relatively simple, both floristically and physiognomically, and production rates are relatively low. Most of the production is shunted belowground (up to 59% to 69% in shortgrass prairies, for example), and indeed a large share of ecosystem energy flows occur in the belowground sector of the system (Andrews et al. 1974). These features of rangeland environments and vegetation are critical to the habitat relations of birds, and restrict avifaunal development to small species assemblages of broadly distributed forms (Wiens 1974a, Cody 1968, 1974).

Much of our information about rangeland birds, especially of the nongame species, is a product of investigations carried out since 1969 as part of the International Biological Program. Both the U.S. Grassland Biome Program and the Canadian Matador Program have concentrated on total system relationships in the North American grasslands. The U.S. effort, centered in Colorado State University, was concentrated on seven grassland types throughout the western part of the country (Van Dyne 1971, Lewis 1971); the Canadian effort, operating out of the University of Saskatchewan, Saskatoon, concentrated its efforts at a single mixed-grass prairie site located north of Swift Current, Sask. (the Matador Site; Ripley 1970).

In this paper we will define rangelands rather broadly, to include not only the grazing lands of the Great Plains and the Intermontane West but more eastern prairies, grasslands, and "pasture" habitats as well. Viewed in this way, "rangelands" are managed or utilized by man to two ends. Primary, of course, is grazing by large domestic herbivores. Grazing exerts a profound influence on rangelands, producing floristic changes toward dominance by plant species characteristic of drier climates (Lewis 1971). Frequently light and moderate grazing intensities stimulate net primary production, (Andrews et al. 1974, Reardon et al. 1974, Vickery 1972). Heavy grazing, on the other hand, presents a problem with analytical techniques in determining net production, but it is generally assumed that there is a reduction since measures of peak standing crop during the growing season are often much lower (Klippel and Costello 1960). One of the main problems is to determine what actually constitutes heavy grazing for various grassland types and even for sites within these types. Thus these various grazing practices can drastically alter vegetation structure, mainly toward lower stature and more patchy species patterns

(Wiens 1973a,b, 1974b). Since birds appear to define their niches largely in terms of habitat structure (Wiens 1969, Balda, this symposium), grazing pressures should be expected to have important consequences for avifaunal composition. Consideration of grazing effects is thus paramount in defining management strategies for nongame birds.

In areas of relatively high rainfall (the former tallgrass prairies of the eastern Great Plains), crop production rather than meat production is the major use of "rangelands." Through much of this region, climax prairies have been replaced by analogs of early successional stages, usually monocultural vegetation "communities" dominated by annual plants subjected to selection for high grain yield (wheat, oats, corn, and the like). In addition to these fundamental alterations of native prairies, agriculture has resulted in the clearing of large areas of previously forested regions in the East, extending grassland or rangeland habitat types, in the form of pastures or fallow fields, far east of former distributions (see, for example, Küchler 1964). The agricultural modifications of rangelands have major effects upon avian communities.

It is within these natural and utilization contexts that decisions regarding the relations of habitat and nongame bird populations must be made. Ideally, such decisions should be based upon ecosystem analyses (Swartzman and Van Dyne 1972), or at least be placed within a systems framework which considers immediate feedback relationships (e.g., Dyer 1973). But to initiate such analyses, land managers must know which bird species are likely to occur in an area, which may numerically dominate the avifauna, how the avian communities may be organized, what functional roles birds may play in the system, and the ways these attributes may be affected by habitat alterations.

In this paper we review information on these features of rangeland bird communities. We emphasize breeding avifaunas, largely because they have received the most study and because information on wintering bird communities in rangelands is scarce. Our approach will stress avian community rather than single species characteristics, as we believe the general patterns to be more instructive for developing future strategies of management. A number of the species characteristic of rangelands have received study, and we reference some of the major studies in Appendix I. We have omitted quail and pheasants (Galliformes) and waterfowl (Anseriformes) from our discussion, as well as raptors

(Falconiformes), which are covered elsewhere in this volume. We thus consider the small nongame birds (mostly Passeriformes) occupying rangeland habitats. We have not attempted to synthesize *all* studies conducted in rangelands, but believe that the patterns which emerge from those we have included are real and general.

THE AVIFAUNA

The Data Base

Our consideration of the avifaunas characterizing various types of rangelands is based primarily upon area-based breeding censuses conducted during the last decade or so. Most of the estimates of species composition and densities were derived using

spot-mapping of singing males (Enemar 1959, Svensson 1970) or territory mapping techniques (Wiens 1969). A comparison of these and other census methodologies in shortgrass prairies is given by Porter (1973). In addition to the studies conducted within the US/IBP and Canadian IBP grassland programs, we have included a number of other breeding studies from rangeland habitat types (as broadly defined above) where the data permitted calculation of species densities (individuals/km²). The locations of the studies we include are depicted in figure 1; the locations are keyed to table 2. In all, 139 plot censuses form the basis for our analysis. We have assigned these in a general fashion to several major habitat types within "rangelands" (see fig. 1). For comparative purposes, we also include several censuses from shrub-dominated communities.

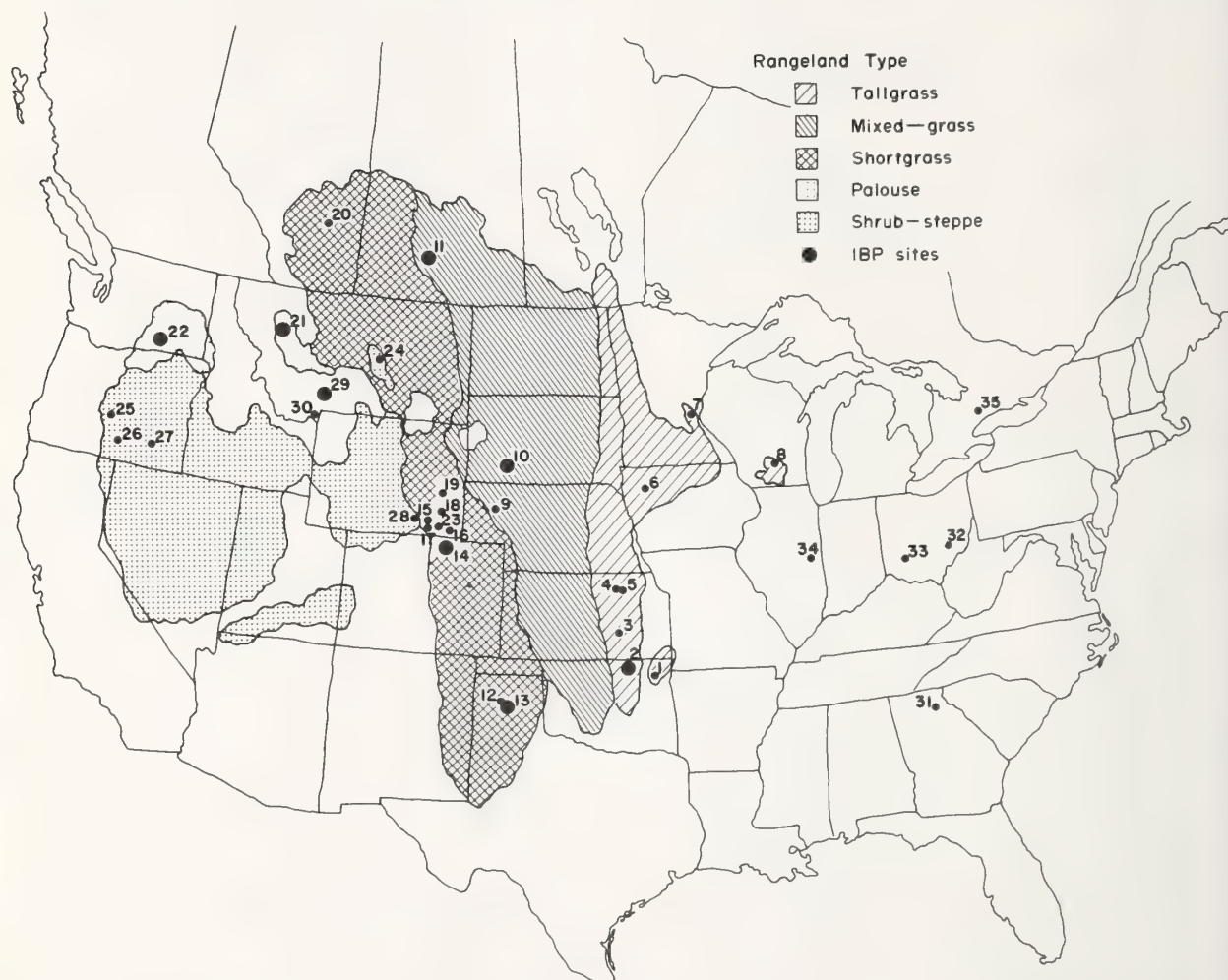


Figure 1. Locations of avian breeding censuses included in this analysis. Census locations are keyed to table 2; large closed circles denote sites included in IBP Grassland Biome studies. Rangeland types generalized from Küchler (1964).

Major Species

Of the 36 breeding species that are represented in the censuses (table 1), 10 species (28%) were recorded with moderate frequency (i.e., more than 10% of the censuses) in single habitat. An additional six

species (20%) were recorded in less than 10% of the censuses conducted in a given habitat type, and 20 breeding species occurred with moderate frequency over at least part of the spectrum of rangeland habitat types. In tallgrass prairies, Eastern Meadowlarks, Grasshopper Sparrows, and Dickcissels occurred

Table 1.--Relative frequencies^{1/} of bird species in breeding censuses conducted in various rangeland types. Galliformes, Anseriformes, and Falconiformes have been omitted

Species	Code	Agriculture (11)	Shrub (5)	Tallgrass (20)	Mixed-grass (19)	Shortgrass (55) ^{2/}	Palouse (12)	Shrub-steppe (14)	Montane (3)
Killdeer (<i>Charadrius vociferus</i>)	K	0.36	--	--	0.05	--	--	--	--
Mountain Plover (<i>Eupoda montana</i>)	MP	--	--	--	--	0.27	--	--	--
Long-billed Curlew (<i>Numenius americanus</i>)	LBC	--	--	--	0.21	--	--	--	--
Upland Plover (<i>Bartramia longicauda</i>)	UP	0.18	--	0.30	0.21	--	--	--	--
Mourning Dove (<i>Zenaidura macroura</i>)	MD	--	--	0.15	--	0.22	0.08	0.07	--
Common Nighthawk (<i>Chordeiles minor</i>)	CN	--	--	0.05	--	0.05	--	--	--
Horned Lark (<i>Eremophila alpestris</i>)	HL	0.36	0.60	--	0.89	0.96	0.75	0.57	0.67
Rock Wren (<i>Salpinctes obsoletus</i>)	RW	--	--	--	--	0.02	--	0.14	--
Sage Thrasher (<i>Oreoscoptes montanus</i>)	ST	--	--	--	--	--	--	0.36	--
Robin (<i>Turdus migratorius</i>)	R	--	--	--	--	--	--	0.07	0.33
Mountain Bluebird (<i>Sialia currucoides</i>)	MB	--	--	--	--	--	--	--	0.33
Water Pipit (<i>Anthus spinoletta</i>)	WP	--	--	--	--	--	--	--	0.33
Sprague's Pipit (<i>Anthus spragueii</i>)	SP	0.09	--	--	0.47	0.02	--	--	--
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	LSh	--	--	--	--	--	--	0.07	--
Yellowthroat (<i>Geothlypis trichas</i>)	Y	--	0.20	--	--	--	--	--	--
Yellow-breasted Chat (<i>Icteria virens</i>)	YBC	--	0.20	--	--	--	--	--	--
Eastern Meadowlark (<i>Sturnella magna</i>)	EM	0.55	0.20	0.80	--	--	--	--	--
Western Meadowlark (<i>Sturnella neglecta</i>)	WM	--	0.60	0.35	1.00	0.75	1.00	0.79	0.33
Bobolink (<i>Dolichonyx oryzivorus</i>)	B	0.27	--	0.20	--	--	--	--	--

Table 1.--Continued

Species	Code	Agriculture (11)	Shrub (5)	Tallgrass (20)	Mixed-grass (19)	Shortgrass (55) ^{2/}	Palouse (12)	Shrub-steppe (14)	Montane (3)
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	RWB	0.45	--	0.15	--	--	--	--	--
Cardinal (<i>Richmondia cardinalis</i>)	C	--	0.20	--	--	--	--	--	--
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	RST	--	0.20	--	--	--	--	--	--
Lark Bunting (<i>Calamospiza melanocorys</i>)	LB	--	0.40	--	0.05	0.56	--	0.29	--
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	SS	0.36	--	0.15	0.32	0.04	--	--	0.33
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)	GS	0.73	0.20	0.80	0.37	0.15	0.08	--	--
Baird's Sparrow (<i>Ammodramus bairdii</i>)	BaS	--	--	--	0.37	0.02	--	--	--
Henslow's Sparrow (<i>Passerherbulus henslowii</i>)	HS	0.09	--	0.10	--	--	--	--	--
Dickcissel (<i>Spiza americana</i>)	D	0.09	--	0.65	--	--	--	--	--
Vesper Sparrow (<i>Poocetes gramineus</i>)	VS	0.64	0.20	0.25	0.26	0.07	0.17	0.93	0.67
Cassin's Sparrow (<i>Aimophila cassinii</i>)	CaS	--	0.60	--	--	0.02	--	--	--
Lark Sparrow (<i>Chondestes grammacus</i>)	LS	--	0.60	--	--	0.04	--	--	--
Sage Sparrow (<i>Amphispiza belli</i>)	SgS	--	--	--	--	--	0.83	0.14	--
Chipping Sparrow (<i>Spizella passerina</i>)	CS	--	0.20	0.05	--	--	--	--	0.33
Clay-colored Sparrow (<i>Spizella pallida</i>)	CCS	--	--	--	--	0.02	--	--	--
Brewer's Sparrow (<i>Spizella breweri</i>)	BrS	--	--	--	--	0.36	0.08	0.86	0.33
Field Sparrow (<i>Spizella pusilla</i>)	FS	0.36	0.20	--	--	--	--	--	--
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	WCS	--	--	--	--	--	--	0.07	0.67
Song Sparrow (<i>Melospiza melodia</i>)	SnS	0.36	--	--	--	--	--	--	--
Chestnut-collared Longspur (<i>Calcarius ornatus</i>)	CCL	0.09	--	--	0.68	0.18	--	--	--
McCown's Longspur (<i>Rhynchophanes mccownii</i>)	ML	--	--	--	0.21	0.56	--	--	--

^{1/}Percent of censuses (given in parentheses) in which species was recorded.

^{2/}Mostly from Pawnee (site 14).

at relatively high frequencies among the plot censuses, with Western Meadowlarks and Upland Plovers more restricted in their occurrence. Western Meadowlarks, Horned Larks, and Chestnut-collared Longspurs were the most characteristic breeding species in the mixed-grass prairies censused, while in shortgrass habitats the latter species was recorded less frequently and McCown's Longspurs and Lark Buntings were more frequently encountered. Western Meadowlarks and Horned Larks were also an important component of breeding avifaunas in Palouse prairies of the Northwest, as were Sage Sparrows. In shrub-steppe habitats, Western Meadowlarks and Horned Larks, though still characteristic, were encountered less frequently, and Vesper Sparrows and Brewer's Sparrows occurred in most censuses. The small set of censuses in montane grasslands recorded Vesper Sparrows, Horned Larks, and White-crowned Sparrows with greatest frequency. Finally, in censuses conducted in various agricultural habitats (e.g., pastures, fallow fields, or "hayfields"), Grasshopper Sparrows, Vesper Sparrows, Eastern Meadowlarks, and Red-winged Blackbirds were recorded most frequently. The rather heterogeneous collection of shrub habitat censuses (five) recorded Western Meadowlarks, Horned Larks, Cassin's Sparrows, and Lark Sparrows most frequently.

A rather small group of species thus characterizes breeding avifaunas in the various types of rangeland habitat. Moreover, while some of these frequently recorded species were restricted in their range of habitat occupancy (e.g., Dickcissels in tallgrass, Red-winged Blackbirds in agricultural situations, Chestnut-collared Longspurs in mixed-grass), many were broadly distributed. Thus meadowlarks of at least one species were encountered at high frequency throughout the spectrum of rangeland habitats, and Horned Larks were lacking only from the censuses in tallgrass prairies. Among the sparrows (Fringillidae), Vesper Sparrows were present in moderate to high frequencies in all habitat types, and Grasshopper Sparrows, Savannah Sparrows, and Brewer's Sparrows occurred in most types. There is, of course, an inherent bias in the frequency values presented in table 1, since censuses of the various habitat types were distributed neither uniformly nor randomly (fig. 1).

The patterns of occupancy described above suggest that some species have similar distributional patterns, while others are mutually exclusive. Wiens (1973a,b) tested

such relationships for a series of 17 plot censuses from US/IBP Grassland Biome Sites (see fig. 1), using Cole's (1949) index of interspecific association. This detects statistically significant deviations from chance co-occurrence of species in either positive or negative directions. The tests indicated that Western Meadowlarks, Lark Buntings, and Horned Larks were positively associated in their distributions, and that Brewer's Sparrows and McCown's Longspurs had a smaller degree of association. Eastern Meadowlarks, Dickcissels, Grasshopper Sparrows, and Upland Plovers formed another loosely associated group which was negatively associated with the former species. As is apparent from table 1, the first group is generally characteristic of shortgrass prairies, while the second is more closely associated with more mesic tallgrass situations. This analysis also revealed that the dominant species tended to be broadly distributed.

Biogeographic Considerations

Distributional patterns such as those discussed above are determined not only by proximate species interactions and habitat selection (what frequently are vaguely referred to as "niche relationships"), but also by the long-term distributional history of a species or group. That such biogeographic considerations may be important in habitat management is evidenced by the dynamic range extensions of several species associated with relatively recent habitat changes, especially in the Great Plains. The biogeography of rangeland avifaunas has been reviewed by Mengel (1970), Udvardy (1963), Hubbard (1973), and Behle (1963). We will not review these studies here, but do draw attention to several points. First, the total set of species "characteristic" of grassland or rangeland areas in North America is small, and the number of species endemic to such biomes is smaller still. Of the species listed in table 1, Mengel lists eight as endemic grassland species and an additional 14 as "secondary" (more widespread) grassland forms. Udvardy's analysis covers a broader range of habitat types; six of the species in table 1 are included in his prairie fauna, while an additional 12 species are scattered over five additional faunal regions or subregions. Second, there has been relatively little taxonomic differentiation of the species characteristic of the central Great Plains. Mengel calculates that there are 1.1 species per genus in the grassland avifauna (compared with 3.6 species per genus in surrounding

nongrassland avifaunas). This suggests a long-term continuity of grassland environments, with little geographic fragmentation which might permit differentiation of isolated parental stocks. This observation is consistent with the broad distributions of many species today (table 1). Third, the biogeographic affinities of rangeland avifaunas to bird faunas of grassland or steppe biomes on other continents are slight; while rangeland avifaunas on different continents may converge in community attributes (Cody 1966), the convergence is ecological rather than taxonomic. This is not unexpected, given the large distributional discontinuities between steppe environments on different continents.

Community Structure

In addition to these current and past patterns of species distributions in rangelands, we may examine various attributes of entire breeding communities of nongame bird populations. Our definition of "community" for the present purposes is a purely operational one: the assemblage of breeding individuals of all species present within a sample plot (i.e., somewhat akin to MacArthur's (1971) view of a community as "any set of organisms currently living near each other and about which it is interesting to talk"). There is, of course, an area effect in such a conception, in that as the area of a sample plot is increased, additional "rare" species, or species occupying large home ranges, will be encountered (e.g., Cody 1974, p. 22). The censuses we have included in our analysis vary in size from 13 acres (5.3 ha) to several hundred acres (over 100 ha); those employed in our IBP analyses were generally 26 acres (10.6 ha). At the level of generalization we will follow below, we feel that area-derived biases are, with a few exceptions, unimportant.

We may ask, then, about the avian community patterns that typify North American rangeland habitats, and about the differences that exist between these various rangeland habitat types. We can characterize these communities according to (i) number of breeding species recorded, (ii) avian densities (breeding individuals per square kilometer, transients ignored), (iii) standing crop biomass (grams of bird per hectare, obtained by multiplying the density of each species by the mean live body weight of the species), (iv) dominance (measured as the percentage of all individuals of all species present

accounted for by individuals of the single most abundant species or of the two most abundant species combined (the "Dominance Index" of Karr 1971)), (v) migratory tendencies (the percentage of species present which undertake seasonal migrations, and are thus not resident in an area throughout the year), (vi) trophic structure (the percentage of individuals belonging to omnivore or carnivore dietary categories), and (vii) body size distributions of the bird species (the percentages of individuals in each of several body size (= weight) categories).

Information on species numbers, densities, biomass, and dominance derived from the census localities of figure 1 is presented in table 2. We should indicate that our assignment of these censuses to the various types of rangeland habitats is to some degree arbitrary; as those who work in rangelands know, the transitions between these habitat types are gradual rather than discrete, with many local variations on the general distributional patterns depicted in figure 1.

Species Numbers

The number of nongame bird species breeding on a census plot in grasslands ranged between one and nine. The mean number of breeding species for the various habitat types ranged from 3.2 (Palouse prairies) to 4.7 (mixed-grass prairies and "agricultural" types), but there are no statistically significant differences in breeding species numbers among the various rangeland habitat types (see also Wiens 1974a). The characteristically low numbers of breeding species in grassland habitats in several areas of the world has also been noted by Cody (1966). Variation in species numbers is greatest in the agricultural habitats, which of course represent a more heterogeneous assemblage of environments than the less disturbed rangelands. Our small set of censuses from shrubby habitats (mostly successional stages in the East or Midwest) suggests that perhaps 10 times as many species may be encountered in plot censuses as in rangelands. The tropical grasslands censused in Panama by Karr (1971) also support substantially more breeding species than their temperate counterparts.

Total Density

The number of breeding individuals per unit area was also markedly uniform among

Table 2.--Characteristics of breeding bird communities in North American rangeland habitat types. Site numbers refer to figure 1; parenthetical values are standard deviations; species codes refer to the common names of the species listed in table 1

Site		Treatment	Plots Sampled	No. of Species	Total Density	Total Biomass	Single-Species Dominance	Dominance Index	Dominant Species	Data Source ^{1/}
No.	Name									
					Ind./km ²	g/ha	%	%		
TALLGRASS PRAIRIES										
1	Inola	Ungrazed	1	2.0	85.0	76.0	80	100	EM,D	1
1	Inola	Grazed	1	3.0	551.0	218.0	72	89	D,EM	1
2	Osage	Grazed	7	4.1	304.2 (131.9)	150.6 (49.8)	45	75	D,EM,GS	2,3,4,5, 6,7
3	Elmdale	Grazed	2	3.5	279.5	122.3	44	72	GS,D	5
4	Donaldson	Grazed	1	3.0	206.0	116.0	45	78	EM,GS	5
5	Riley	Grazed	3	6.3	456.9 (33.4)	305.7 (27.6)	31	53	RWB,D	8,9,10
6	Iowa	Ungrazed	1	5.0	257.1	--	31	62	B,GS	11
7	Anoka ^{2/}	1-yr field	1	1.0	89.0	21.4	100	100	VS	12
7	Anoka ^{2/}	3-yr field	1	1.0	89.0	21.4	100	100	VS	12
7	Anoka ^{2/}	10-yr field	1	2.0	237.2	45.5	56	100	VS,CS	12
8	Fitchburg	Grazed	3	6.0	494.2 (111.9)	166.6 (33.3)	38	68	SS,GS	13
Tallgrass		\bar{X}		4.1	329.2	164.9	48.3	74.6		
		S		1.5	158.5	76.3	18.2	14.8		
MIXED-GRASS PRAIRIES										
9	Sandhills	Grazed	1	3.0	101.0	60.0	45	78	WM,HL	5
9	Sandhills	Ungrazed	1	5.0	317.0	113.0	52	77	GS,LB	5
10	Cottonwood	Grazed	3	2.7	154.0 (14.3)	84.2 (24.9)	64	95	HL,WM	2,3,4,5, 6,7
10	Cottonwood	Ungrazed	5	5.2	204.3 (62.1)	156.8 (52.4)	50	79	GS,WM	2,3,4,5, 6,7
11	Matador	Grazed	4	5.8	410.0 (77.4)	106.6 (24.6)	45	70	CCL,ML, HL	14
11	Matador	Ungrazed	5	6.8	232.4 (53.0)	76.2 (14.9)	35	59	SP,BaS	14
Mixed-Grass		\bar{X}		4.7	236.5	99.5	48.5	76.3		
		S		1.6	112.1	34.2	9.6	11.8		
SHORTGRASS PRAIRIES										
12	Amarillo	Grazed (grass-shrub)	3	4.7	345.1 (82.4)	127.4 (35.2)	36	65	LS,CaS, HL	15,16,17
13	Pantex	Ungrazed	3	3.0	167.5 (38.8)	93.1 (17.0)	54	88	HL,WM	2,3,4,5, 6,7
13	Pantex	Grazed	5	2.8	343.2 (62.0)	139.9 (21.4)	69	89	HL,GS,WM	2,3,4,5, 6,7

Table 2.--Continued

Site		Treatment	Plots Sampled	No. of Species	Total Density	Total Biomass	Single- Species Dominance	Dominance Index	Dominant Species	Data Source/
No.	Name									
					Ind/km ²	g/ha	%	%		
14	Pawnee	Heavy winter grazed	4	4.3	295.2 (51.1)	94.4 (5.5)	51	76	LB,HL	18,3,4,6
14	Pawnee	Heavy summer grazed	4	3.8	246.7 (40.9)	81.1 (16.8)	52	86	ML,HL	18,3,4,6
14	Pawnee	Light winter grazed	4	5.5	272.4 (51.1)	111.7 (45.6)	34	62	HL,LB	19,20,21
14	Pawnee	Moderate winter grazed	4	6.2	259.7 (74.7)	95.2 (28.2)	39	63	HL,LB	19,20,21
14	Pawnee	Heavy winter grazed	4	5.5	268.9 (65.6)	99.4 (16.4)	37	66	LB,HL	19,20,21
14	Pawnee	Light summer grazed	4	5.8	278.5 (13.9)	110.2 (7.6)	43	68	LB,ML	19,20,21
14	Pawnee	Moderate summer grazed	4	5.3	228.8 (38.9)	95.7 (23.8)	51	80	HL,LB	19,20,21
14	Pawnee	Heavy summer grazed	4	4.5	287.5 (72.5)	112.6 (32.5)	57	88	HL,ML	19,20,21
15	Laramie	Grazed (grass- shrub)	4	4.3	283.4 (57.8)	98.9 (27.9)	55	81	ML,HL,VS	22,23,24
16	Cheyenne	Grazed	2	3.0	526.3 (55.9)	176.9	50	98	HL,ML	25
17	Laramie	Grazed	3	2.7	344.3 (66.1)	116.1	53	97	HL,ML	25
18	Laramie	Light grazed	1	2.0	263.0	74.0	57	100	ML,HL	5
19	Wheatland	Light grazed (rocky)	1	3.0	74.7	49.3	57	82	WM,RW	1
19	Wheatland	Heavy grazed	1	6.0	468.4	162.0	67	83	LB,HL	1
20	Hand Hills	Ungrazed	1	5.0	271.6	70.6	43	74	SP,BaS	26
20	Hand Hills	Grazed	1	5.0	138.9	44.8	49	71	CCL,HL	26
Shortgrass		\bar{X}		4.3	282.3	102.8	50.2	79.8		
		S		1.3	102.2	33.5	9.7	12.0		

Table 2.--Continued

Site		Treatment	Plots Sampled	No. of Species	Total Density	Total Biomass	Single-Species Dominance	Dominance Index	Dominant Species	Data Source ¹
No.	Name									
					Ind./km ²	g/ha	%	%		
PALOUSE PRAIRIES										
21	Bison	Grazed	1	3.0	144.4	78.6	51	95	GS,WM	3,4,5
22	ALE	Ungrazed shrub-grass	9	3.0	202.6 (53.8)	80.2 (24.2)	56	87	SgS,HL	5,6,7,27
22	ALE	Ungrazed bunch-grass	1	3.0	204.4	94.2	60	84	HL,WM	27
22	ALE	Ungrazed hopsage	1	3.0	269.4	112.2	41	78	HL,SgS	27
Palouse		\bar{X}		3.0	205.2	91.3	52.0	86.0		
		S		0.0	51.1	15.6	8.2	7.1		
SHRUB-STEPPE										
23	Laramie	Grazed	3	2.7	109.6 (33.7)	33.9	55	93	HL,VS	25
24	Winnett	Grazed	4	4.5	362.8 (58.1)	77.4 (18.1)	58	85	BrS,VS	28,29
24	Iverson	Ungrazed	13	4.3	335.6 (74.5)	74.1 (14.7)	53	88	BrS,VS	28,29
24	Iverson	Partial spray	1	--	408.6	84.9	48	--	BrS,VS	29
24	Winnett	Strip spray	1	--	394.5	81.1	50	--	BrS,VS	29
24	Winnett	Total spray	1	--	267.6	62.2	60	--	VS,BrS	29
25	Cabin Lake	Grazed	1	4.0	459.0	75.0	55	87	BrS,SgS	5
26	Chewaucan	Lightly grazed	1	5.0	139.0	72.0	41	76	SgS,WM	5
27	Steens Mountain Shrub-steppe	Lightly grazed	1	4.0	192.0	54.0	53	79	VS,RW	5
		\bar{X}		4.1	296.5	68.3	52.6	84.7		
		S		0.8	125.5	16.0	5.7	6.2		
MONTANE GRASSLANDS										
28	Snowy Range	Grazed	2	3.0	79.1 (7.0)	19.3	55	89	WP,WCS	25
29	Bridger	Lightly grazed	1	4.0	108.8	40.1	49	68	VS,R	3,4,5
30	Cliff Lake Montane	Ungrazed	1	6.0	552.0	125.0	46	70	SS,VS	5
		\bar{X}		4.3	246.6	61.5	50.0	75.7		
		S		1.5	264.9	56.0	4.6	11.6		

Table 2.--Continued

Site		Treatment	Plots Sampled	No. of Species	Total Density	Total Biomass	Single- Species Dominance	Dominance Index	Dominant Species	Data Source ^{1/}
No.	Name									
<hr/>										
					Ind./km ²	g/ha	%	%		
<hr/>										
AGRICULTURAL										
31	Athens	1-yr field	1	2.0	79.1	39.6	62	100	GS,EM	30
31	Athens	3-yr field	1	2.0	210.1	90.1	71	100	GS,EM	30
32	SE Ohio	Meadow	1	6.0	280.6	59.6	62	84	GS,VS	31
32	SE Ohio	Pasture	1	4.0	84.5	26.5	42	71	GS,FS	31
33	SW Ohio	Small grain	1	2.0	45.2	19.7	50	100	RWB,GS	31
33	SW Ohio	Meadow	1	8.0	244.3	105.6	47	69	GS,EM	31
33	SW Ohio	Pasture	1	7.0	332.4	137.6	53	75	GS,EM	31
34	Illinois	Bare ground	1	11.0	140.0	80.5	--	50	--	32
35	Ontario	Pasture	5	5.2	279.7 (89.7)	120.6	46	60	SS,EM	33
35	Ontario	Hay fields	5	7.2	502.1 (153.6)	153.8	41	54	SS,GS	33
20	Hand Hills	Mowed	1	3.0	197.6	42.1	63	94	CCL,SP	26
20	Hand Hills	Fallow	1	1.0	37.0	12.5	100	100	HL	26
20	Hand Hills	Seeded	1	2.0	30.9	9.9	80	100	HL,VS	26
Agriculture		\bar{X}		4.7	189.5	69.1	59.8	81.3		
		S		3.0	139.3	49.2	17.4	19.1		
SHRUBS										
31	Athens	4-yr	1	7.0	536.1	167.9	32	55	FS,GS	30
34	Illinois	Early shrub	1	47.0	1705.0	782.1	--	21	--	32
34	Illinois	Late shrub	1	74.0	1875.0	966.0	--	17	--	32
7	Anoka ^{2/}	10-yr	1	2.0	237.2	45.5	56	100	VS,CS	12
7	Anoka ^{2/}	18-yr	1	2.0	187.8	32.0	63	100	CS,VS	12
Shrub		\bar{X}		42.6	1372.0	638.7	--	--		
		S		33.7	728.9	417.9				
TROPICAL (PANAMA)										
	Dry grass- land	Grazed	1	31.0	305.0	101.7	--	62	--	32
	Wet grass- land	Grazed	1	33.0	330.0	127.8	--	43	--	32
	Dry grass- land	Ungrazed	1	35.0	250.0	98.6	--	42	--	32
	Wet grass- land	Ungrazed	1	38.0	445.0	116.2	--	59	--	32

Table 2.--Continued

Site		Treatment	Plots Sampled	No. of Species	Total Density	Total Biomass	Single- Species Dominance	Dominance Index	Dominant Species	Data Source ¹
No.	Name									
Tropical	\bar{X}	34.2	332.5	111.1	--	51.5				
	S	3.0	82.1	13.5	--	10.5				

¹/ 1, Wiens, unpublished; 2, Wiens 1971; 3, Wiens 1973a; 4, Wiens 1973b; 5, Wiens 1974b; 6, Wiens et al. 1972; 7, Wiens et al. 1974; 8, Zimmerman 1965; 9, Zimmerman 1966; 10, Zimmerman 1967; 11, Kendeigh 1941; 12, Mitchell 1961; 13, Wiens 1969; 14, Maher 1973; 15, Allen 1938; 16, Allen & Sime 1939; 17, Allen & Sime 1940; 18, Wiens 1970; 19, Giezantanner 1970; 20, Ryder 1972; 21, Porter & Ryder 1974; 22, Mickey 1939; 23, Mickey 1940; 24, Mickey 1941; 25, Finzel 1964; 26, Owens & Myres 1973; 27, Rotenberry, unpublished; 28, Feist 1968; 29, Best 1972; 30, Johnston & Odum 1956; 31, Good & Dambach 1943; 32, Karr 1971; 33, Speirs & Orenstein 1967.

²/ Census not included in habitat type average.

the various rangeland types, with average densities per type ranging from 185 (Palouse prairies) to 329 individuals/km² (tallgrass prairies). There was considerable variation among censuses, however, preventing the definition of statistically significant differences between types. Certainly no sharp trend for the more productive areas (tallgrass and perhaps montane grasslands) to support more individuals than xeric habitats emerges. Breeding densities in the agricultural types were relatively low, those in shrubby habitats much greater than in any of the rangeland situations. Tropical grasslands, despite the greater diversity of species, apparently contained only slightly more individuals than bred in temperate tallgrass prairies or arid shrub-steppe.

Total Biomass

While species numbers and densities exhibited no well-defined changes among the range of rangeland habitat types, Wiens (1974a) found that among a series of 33 censuses in grassland-shrub-steppe habitats, tallgrass prairies consistently supported more biomass than shortgrass, Palouse prairies, or shrub-steppe, while shortgrass and

Palouse contained more biomass than shrub-steppe plots. This trend is even more well-defined among the larger series of censuses represented in table 2. Biomass generally decreased in the order tallgrass--mixed-grass, shortgrass--Palouse--shrub-steppe, montane, a sequence generally agreeing with the gradient of decreasing precipitation--decreasing primary production among these habitat types. Agricultural plots supported a relatively low avian biomass, similar to that in shrub-steppe and montane areas. Biomass was considerably greater in the inadequate sample of shrubby habitats, but that in the tropical grasslands was similar to that in temperate mixed-grass or short-grass prairies.

These density and biomass values suggest that the two community attributes are not closely related, which at first glance may seem counterintuitive. In figure 2 we have plotted mean density and biomass values for breeding avifaunas, using the data of table 2. A general tendency for biomass to increase with increasing density is apparent (fig. 2), but the patterns for the different rangeland types are more instructive. In all types there is a general tendency for biomass to increase with density, and in tallgrass,

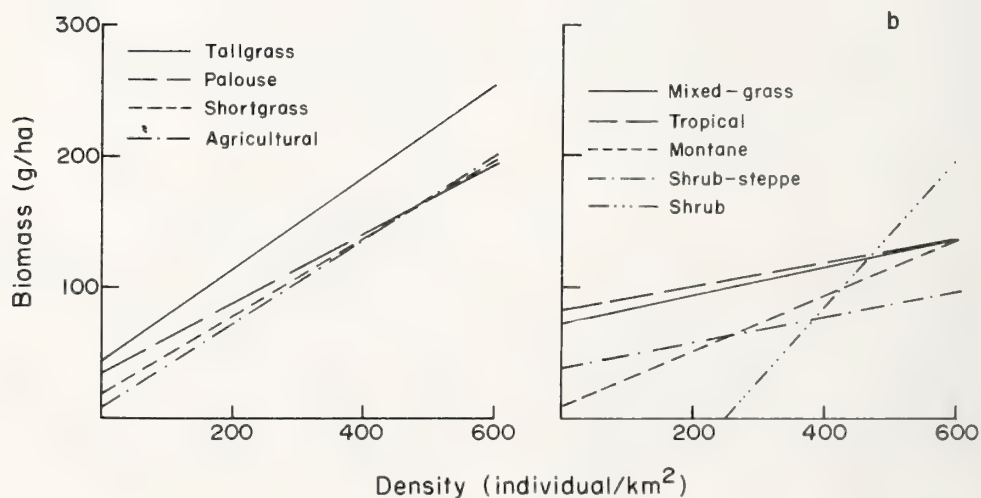
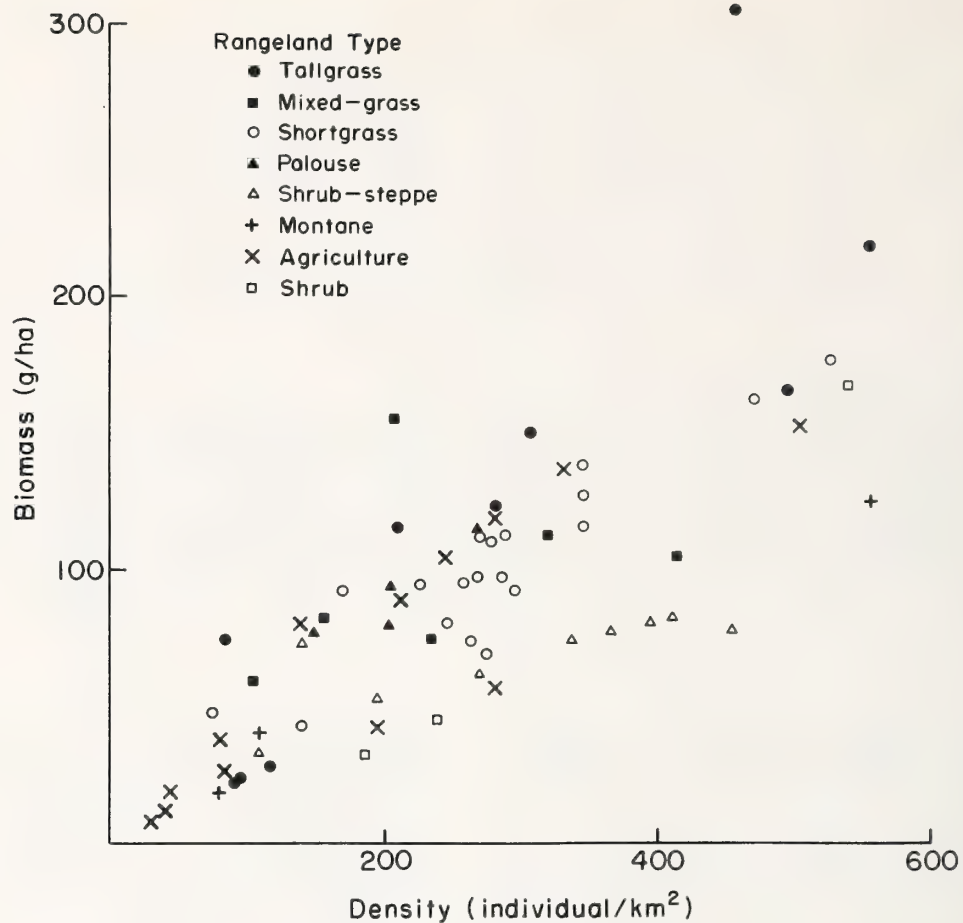


Figure 2. Relations between breeding densities and standing crop biomasses in breeding avifaunas in rangelands. Least-squares regression lines for each rangeland type are given in part B.

shortgrass, shrub-steppe, agricultural, and shrub types this trend is statistically significant. But note the slopes of the regression lines. The rate of increase in tallgrass prairies, shortgrass, and agricultural types is high and similar among the types; the rate of increase in mixed-grass prairies, Palouse, the tropical grasslands in Panama, and shrub-steppe is much lower, but again quite similar among those types. Of the latter group, only the shrub-steppe relations are statistically significant, while all those of the former group follow significant trends. The absence of strong relations in the latter group suggests that these results may be spurious, but the patterns are nonetheless intriguing. The rate of increase in biomass with increasing density relates to a function of the sizes of the individuals which account for the density increases; the patterns depicted in figure 2 may be associated with differences in body size distributions in the avifaunas of the different types (discussed below).

Species Dominance

Since rangeland habitats support a relatively small breeding avifauna, one might intuitively expect more of the individuals present to be concentrated in fewer species than in more species-rich habitats. The census data of table 2 suggest that, on the average, roughly half of the individuals present belong to the single most abundant species (regardless of what that species is), while 75% to 88% of the individuals are included in the two most abundant species. Significant variations between the various rangeland types are not apparent. Dominance of the single most abundant species is related to species number in figure 3. Note that high dominance is associated with low species diversity; the line in figure 3 represents the situation when all species are equally abundant, and diversity is maximal (i.e., dominance is the lowest possible). While dominance does decrease as species richness increases, it nonetheless diverges strongly from the minimum dominance possible. Thus a good deal of the community structuring in rangelands is accounted for by one or two breeding species: The avifaunas are strongly dominated. The species dominating each census site or habitat are listed in table 2, and in general these agree with the "important" species earlier defined in terms of frequency of occurrence (table 1).

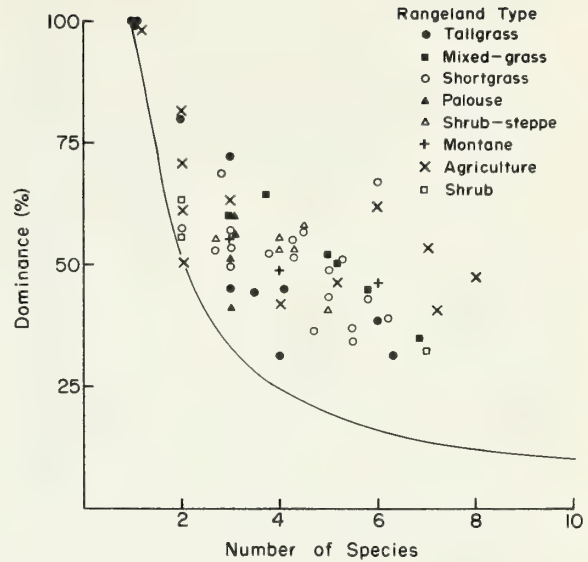


Figure 3. Relation between the number of breeding species and the "dominance" of the most abundant species in various rangeland avifaunas. The curve represents the minimum dominance theoretically attainable when all species present are equally abundant.

Migratory Tendencies

Assessment of the degree of expression of migratory or seasonal residency tendencies among the species represented in the censuses of table 2 has not been undertaken, but Wiens (1974a) did make such a determination for a series of plot censuses widely distributed through grasslands (including Palouse and shrub-steppe but omitting montane) in the United States. The results of this analysis (table 3) indicated that a significantly greater proportion of the breeding species were migrants in tallgrass and mixed-grass prairies than in shortgrass, while shrub-steppe avifaunas contained significantly more migratory species than either shortgrass or tallgrass habitats. These patterns should be expected to be related to the availability of food supplies (chiefly seeds) during the winter, and suggest that winter seed availability may be least in shrub-steppe, somewhat "intermediate" in tallgrass, mixed-grass, and Palouse habitats, and greatest in

Table 3.--Ecological attributes of breeding avifaunas of rangeland habitat types (from Wiens 1974a)

Type	Percent of Breeding Species Migratory ^{1/}	Percent of Individuals		Percent of Individuals with Body Size		
		Omnivore ^{2/}	Carnivore	Small ^{3/}	Medium ^{3/}	Large ^{3/}
Tallgrass	66.4	64.6	35.4	34.6	29.8	35.6
Mixed-grass	65.4	70.0	30.0	32.4	37.8	30.0
Shortgrass	42.3	83.6	16.4	5.9	82.6	11.4
Palouse	61.3	73.7	26.3	45.7	27.3	27.0
Shrub-steppe	95.3	47.3	52.7	70.3	15.3	14.0

^{1/} Wintering range separated from breeding area by at least 200 km.

^{2/} Omnivore = animal prey comprises <75% of diet, by dry weight.

^{3/} Small = \leq 25 g/individual; medium = 26-80 g/individual; large = >80 g/individual.

shortgrass prairies. Actual seed availabilities in these habitat types are yet undetermined.

Trophic Structure

One may expect that these projected patterns of food availability-migratory tendencies might be coupled to patterns of dietary habits of the breeding species. Wiens' (1974a) analysis (table 3) in fact suggests that during the breeding season, omnivory (i.e., some dependence on seeds during the breeding season, which is presumably coupled with a nearly complete seed diet during winter) is greater in shortgrass bird populations than elsewhere in the grasslands, while most of the individuals breeding in shrub-steppe habitats (where migration is nearly complete) are carnivorous.

Body Size Distributions

The results presented above (table 2) indicated that while species numbers and total density were generally similar over a wide range of rangeland habitats, biomass decreased from mesic toward xeric areas. This implies that there may be basic differences in the way biomass is partitioned among different-sized species in these areas. The analysis

of Wiens (1974a, table 3) indicates that in tallgrass and mixed-grass prairies there are roughly equal densities of the arbitrarily defined small, medium, and large size classes, but in shortgrass habitats, medium-sized species predominate. In shrub-steppe the lower biomass reflects the abundance of small-sized species. Thus, the changes in avian biomass from shrub-steppe through shortgrass to tallgrass prairies apparently stem from shifts in dominance by different-sized species rather than changes in total numbers of individuals of all species. Comparative data which would lend some perspective to these patterns are scarce. In northwestern coniferous forests, small species (less than 10 g body weight) dominate, a size class which is totally lacking in rangelands. The analysis of McNaughton and Wolf (1973, p. 376) of size distribution changes during secondary succession in Georgia (the census data of Johnston and Odum 1956) indicates that in early successional stages, biomass is partitioned among very large or small size classes. As succession proceeds, the large class becomes less important and smaller size classes are added, with the result that individuals are spread more evenly among the various size classes, and mean individual size decreases.

Avifaunal Stability

It is critical to determine how stable these avifaunal patterns are through time, since the approach to "managing" fluctuating populations or communities will likely be quite different from that applied to stable systems. Stability or instability may be considered in several time frames, each of which has distinct ecological implications. At one scale, flux in the density or presence of bird populations during the breeding season may be critical. The assumption of plot censuses is that the breeding densities sampled are stable, but in fact densities ebb and flow within breeding populations due to territorial shifts, mortality, or early abandonments of nestings or late renestings (see, e.g., Wiens 1969). Perhaps the most careful documentation of these shifts in population densities is provided by Ryder and his students (Porter and Ryder 1974, Ryder 1972) from studies on the shortgrass prairie site of the US/IBP Grassland Biome Program in northeastern Colorado (the Pawnee Site). Their repeated plot censuses (fig. 4) reveal considerable variation in the densities of all of the dominant breeding species at Pawnee. Insofar as single breeding plot censuses are conducted at different times during the local phenology of several avian communities, error may be inherent in plot census comparisons.

At another time scale, *inter-seasonal* variations in species abundances may be considerable. We have already noted (table 3) the expression of migratory tendencies (= seasonal residency) among the breeding bird species of most rangeland types. These seasonal variations may be examined in greater detail from information obtained in seasonal roadside censuses conducted at three IBP Grassland Biome sites, following standard procedures (Robbins and Van Velzen 1967, Rotenberry and Wiens 1975). We may calculate *species turnover* (T), the net change in species composition from one season to the next, by:

$$T = \frac{S_i + S_{i+1}}{S_c + S_i + S_{i+1}} \quad (1)$$

where S_i = number of species unique to count i , S_{i+1} = number of species unique to the next successive count, and S_c = number of species common to both counts. The values (table 4) indicate a relatively high rate of seasonal species turnover at all three sites. Spring-summer changes were generally less than between other seasons, probably due to the early arrival of breeding species. Summer-to-spring seasonal turnovers were highest at the mixed-grass site, reflecting the low number of wintering species present in this northern site. Closer examination of these values (Wiens et al. 1974) reveals that most of the site differences stem from the effects of "rare" or low-frequency species, but the basic patterns remain. Rangeland avifaunas thus may be characterized by substantial changes in species compositions with seasonal progressions.

A third time scale considers annual or year-to-year variations in breeding bird populations. Definition of annual flux requires a series of successive plot censuses; to date, the most complete information of this sort comes from the IBP grassland studies in the United States and Canada. The repeated plot censuses conducted at the Pawnee shortgrass site (fig. 4) indicate not only within-season changes in species densities, but substantial annual differences in breeding densities as well (Giezantanner and Ryder 1969). Similar magnitudes of species density changes have been recorded by Whitney (personal communication) in standardized roadside censuses conducted over a mixed-grass prairie habitat near the Cottonwood Site in South Dakota from 1967 to 1974 (fig. 5). In Whitney's surveys, the dominant species appeared to undergo greater variations in abundance in relation to the total avian community than species breeding at generally low densities, a relationship also apparent in the Pawnee studies (fig. 4). In both cases, however, the species composition of the breeding season avifauna remained stable from year to year; only the densities of these "characteristic" species varied (see also Wiens 1974a,b). Thus the moderate annual turnover in breeding species composition indicated in table 4 apparently reflects the influences of "rare" species encountered on the roadside censuses; the species composition of the "dominant" segment of the breeding avifauna changes little from year to year for a given site.

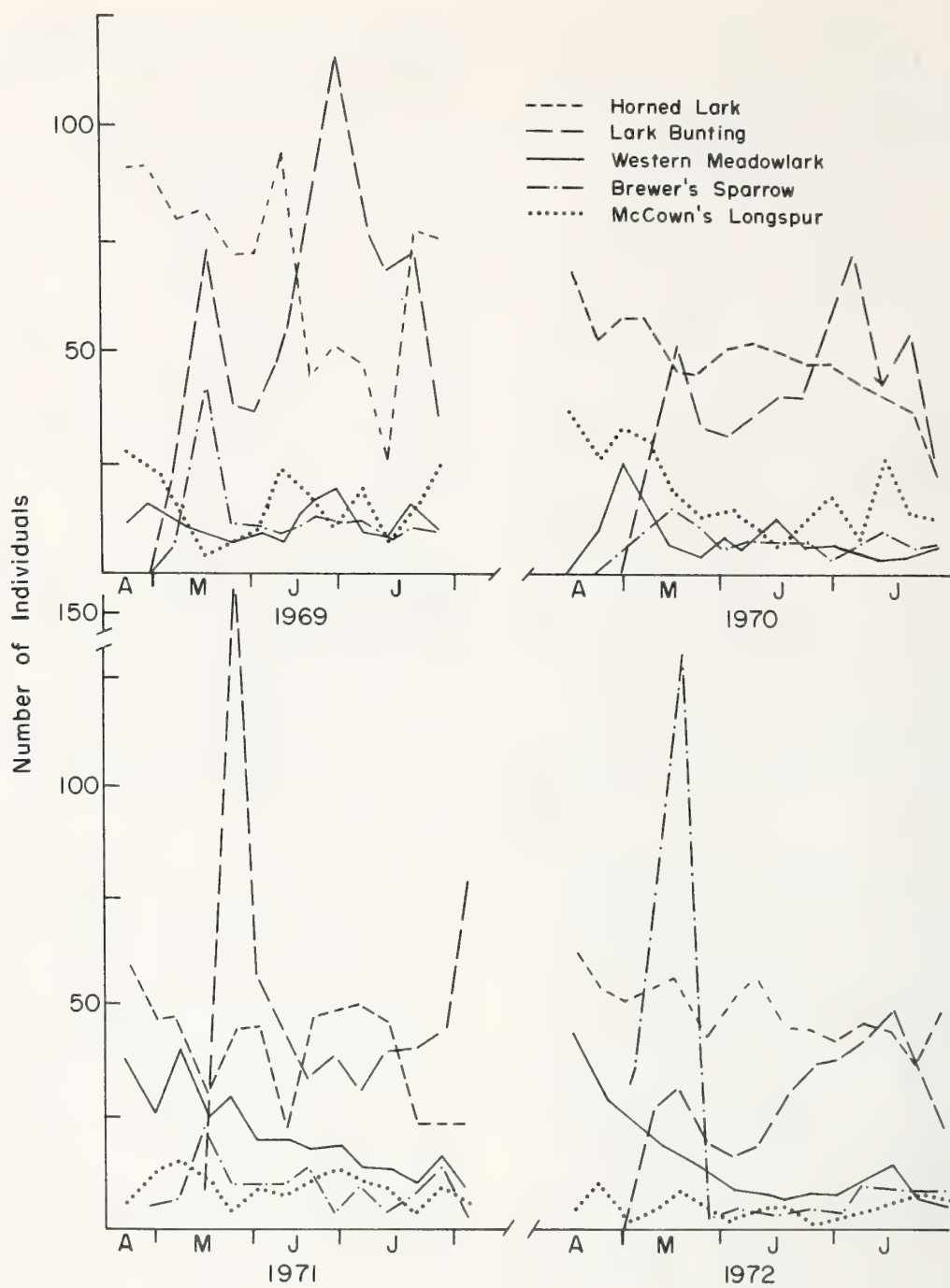


Figure 4. Variations in densities of major breeding species presented by month in the shortgrass prairies of northeastern Colorado during the breeding seasons of four years. From Porter and Ryder (1974).

Table 4.--Inter-seasonal turnover in species composition recorded in roadside censuses at IBP Grassland Biome sites. Values are means of species turnover (T) (see text); standard deviations in parentheses (from Wiens et al. 1974).

Type	Site	Species turnover (T)				
		Spring-Summer	Summer-Fall	Fall-Winter	Winter-Spring	Annual ^{1/}
Tallgrass	Osage	54 (8.2)	62 (7.0)	72 (13.4)	72 (2.8)	54 (1.4)
Mixed-grass	Cottonwood	47 (11.8)	82 (6.2)	86 (6.4)	95 (2.1)	59 (5.7)
Shortgrass	Pantex	37 (3.2)	63 (3.5)	76 (--)	76 (--)	78 (4.2)

^{1/}Percent of species recorded in successive years (breeding season).

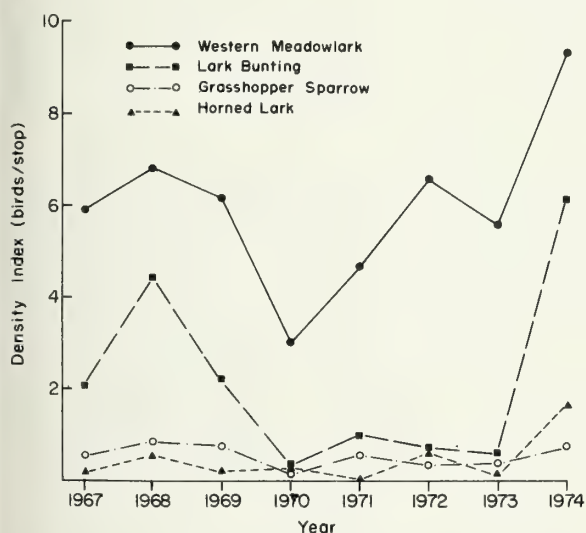


Figure 5. Annual variations in abundance of major breeding species in South Dakota mixed grasslands. Data from roadside censuses conducted during the height of breeding season by Whitney (pers. comm.) near Cottonwood, South Dakota.

Considerable annual variation is also apparent when one examines total avian densities and biomass in census plots. Values for several sites and grazing intensities studied during the US/IBP Grassland Biome

investigations (Wiens et al. 1974) are depicted in figure 6. None of the plots appear "stable" in density or biomass, and there is little yearly agreement in between-site trends (even among different grazing treatments at the same location). Most instructive, perhaps, are the values from "replicate" plot censuses which were conducted in secondary 10.6-ha census plots located within the same field and habitat type and at the same time as the primary census plots. While both plots within a given field at the same site agree in the direction of annual change, the magnitude of this change often differs considerably. Thus annual variations cannot be defined precisely, even within a given 100-ha "pasture."

The magnitudes of annual variations in breeding densities can be measured at a broader level using the coefficient of variation (CV) of annual density estimates for all plots which were sampled over successive years (table 5). The values for mean CV of total density are relatively similar (and comparatively large) for the various rangeland types, with shrub-steppe densities exhibiting perhaps the greatest "instability." Densities of the most dominant breeding species at the sites exhibit generally greater annual variation than the total assemblage of breeding species (table 5), especially in tallgrass prairies (this is probably a reflection of the frequent dominance of Dickcissels, which are notably erratic in their local and regional distributions, in tallgrass sites). Again, the total breeding community appears to be more stable, annually, than populations of the dominant species.

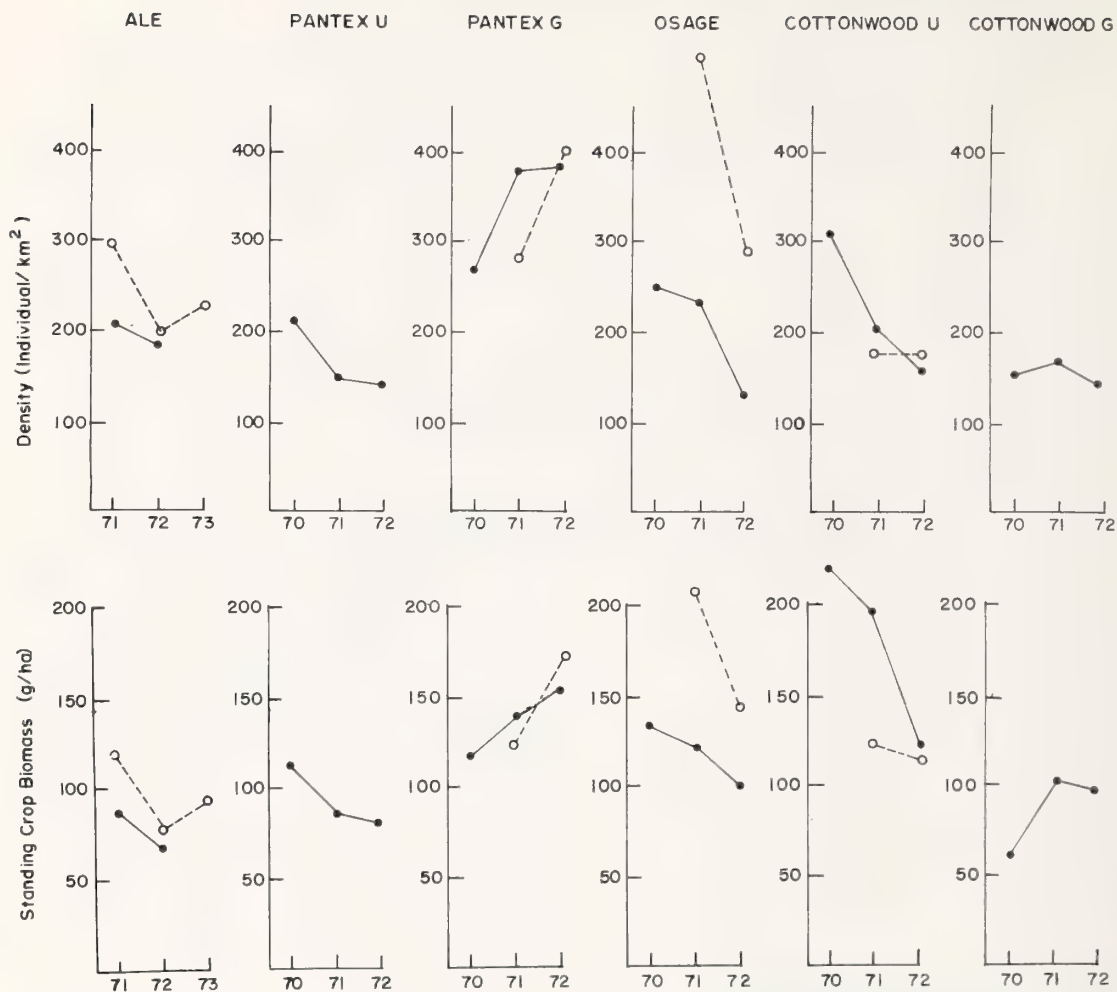


Figure 6. Annual variations in avian density and biomass in IBP Grassland Biome plots. Solid and dashed lines represent values for "replicate" plots located in the same grazing treatment pasture. From Wiens et al. (1974).

Table 5.--Coefficients of variation (CV) of breeding densities and biomass in rangeland habitat types censused over successive years. Values are mean CV with standard deviations in parentheses

Type	N	Annual coefficient of variation ^{1/}	
		Total density	Density of dominant species
Tallgrass	8	16.3 (16.7)	37.2 (40.7)
Mixed-grass	12	15.5 (10.0)	20.7 (12.7)
Shortgrass	25	16.7 (8.9)	28.4 (18.1)
Palouse	3	13.9 (9.1)	20.5 (6.1)
Shrub-steppe	9	20.4 (13.8)	13.9 (9.2)
Montane	1	8.8 (--)	20.2 (--)

$$1/ CV = \frac{100s}{\bar{X}}$$

How may these substantial yearly fluctuations in abundance and biomass in rangeland avifaunas be explained? We expected to find close relationships to contemporary climates, but no clear patterns seem apparent. Since adjacent census plots subjected to different grazing regimes frequently exhibited different yearly changes (fig. 6), it is difficult to imagine close interactions with climatic variables. At the shortgrass site in Texas (Pantex), for example, the extremely low rainfall during 1970 and the first half of 1971 might have been expected to lower 1970 breeding success and lead to lower densities in 1971. But on the grazed plot, total density was considerably higher in 1971 (fig. 6), largely because of a tremendous increase in Horned Lark density. On the ungrazed plot a short distance away, however, total density and Horned Lark density were lower in 1971. Determination of close relationships is rendered more difficult, of course, by the fact that in most rangeland habitats a good share of the populations are seasonal migrants, so that their abundance at a site in any given year may result from present and past conditions at that site as well as elsewhere in the species' range.

The possibility may also exist that these annual fluxes in avian densities are not due to real changes in population sizes but to differences in local dispersion. Thus the number of individuals in an area of, say, several square kilometers may change little between years, but 0.1 km² plots sampled from this population may record considerable changes due to yearly changes in dispersion patterns within the population largely unrelated to local plot conditions. Consider this analogy: It is as if individual territories were checkers on a checkerboard with walled edges. Every year the board is shaken to redisperse the checkers, and while the total number of checkers on the board may remain the same, the number encountered on any sample plot of, say, eight squares may change. Further, the direction of changes on adjacent eight-square plots might well differ. Obviously, the extent of such change would be related to the packing of checkers (territories) on the board; with a densely packed board there would be little room available for yearly redispersal, and "plot" counts would indicate relative stability. This argument presumes that breeding rangeland populations may not normally exist at maximum density or "carrying capacity," a suggestion developed more fully elsewhere (Wiens 1974a).

There is yet another scale of temporal variation in rangeland avifaunas which must be mentioned. Left alone and under favorable environmental conditions, rangeland habitats will undergo ecological succession toward shrub, savannah, or woodland ecosystem types. These long-term changes must unavoidably affect bird populations. In most rangeland ecosystems of western North America such successional changes are of little consequence, since the low precipitation regimes preclude successional change or extend its time frame by literally centuries. However, in more eastern expressions of "rangelands," such as mesic tallgrass prairies or pockets of grassland carved from deciduous forest, succession may alter a pasture into a shrub or early woodland community within a decade or two. The studies of Johnston and Odum (1956) in Georgia, Beckwith (1954) in Michigan, and Mitchell (1961) in Minnesota provide some indication of the effects of such successional changes on breeding bird populations. With shrub invasion there is a dramatic increase in the number of breeding species, total density, and standing crop biomass, and a decrease in species dominance. Few of the "characteristic" rangeland species (table 1) persist beyond early shrub stages. While these results are not unanticipated, they do demonstrate the sensitivity of rangeland bird communities to major alterations in the vegetational habitat, as occur during succession.

Effects of Habitat Utilization by Man

Succession represents a natural modification of habitat features, but more important, especially through the main portions of western North American rangelands, are manipulations exercised by man. Human utilization or manipulation of rangelands may be considered in three categories: grazing of large domestic herbivores (chiefly cattle), crop production, and, increasingly in western shrub-steppe, herbicidal spraying for shrub removal.

Grazing Effects

Grazing is perhaps the major utilization of rangeland habitats. Its effects on breeding avifaunas, however, are not uniform nor easily defined, primarily because grazing varies so much in its local intensity and because of the general difficulties in unraveling cause-effect relationships in rangeland avifaunas. The most careful attempts to

document grazing effects have been undertaken within the IBP studies, where plots exposed to differing intensities of grazing are available at several sites. An analysis of 1970 data (Wiens 1973a) indicates that grazing influences avifaunal structure to differing degrees at different sites. At the short-grass Pantex Site, for example, grazed and ungrazed plots were quite similar in the composition of breeding bird communities, while heavily grazed and lightly grazed treatments at the mixed-grass prairie site (Cottonwood) differed markedly. At the shortgrass Pawnee Site in Colorado, the season of grazing (winter or growing season) appeared to influence avian communities more than the intensity of grazing. Over the range of grassland sites compared, ungrazed or lightly grazed plots generally appeared to have slightly more breeding species than heavily grazed plots; at two sites (Pawnee and Cottonwood), total density and standing crop biomass were greater in the lightly grazed plots. These alterations in avifaunal patterns were probably mediated largely through the effects of grazing on vegetation structure and composition. Thus the degree of vegetational similarity between heavily grazed and lightly grazed or ungrazed plots at the sites was generally paralleled by the extent of similarity in breeding bird populations: Where the grazing regime affected vegetational composition only slightly, the bird species composition of the treatment plots seemed also unaffected. On the other hand, where grazing produced marked changes in vegetation, there were accompanying major shifts in avian community composition, generally toward closer resemblance to avian communities in more xeric locations. As a result, plots of similar vegetation patterning at widely separated sites in the grasslands may resemble each other much more (in terms of avifauna) than plots of differing vegetation structure located across a fence line from one another at the same site.

These avian community responses to grazing pressures are of course functions of the changes in species populations and distributions. The findings of Owens and Myres (1973) in their study of Alberta *Festuca*-dominated shortgrass prairies are representative:

"Under grazing practices which are aimed at maintaining the range in good condition, the full range of prairie passerines may be expected to occur. Under grazing conditions tending to be heavier than normal, chestnut-collared

longspurs and horned larks will predominate, while under grazing conditions lighter than normal, Sprague's pipits and Baird's sparrows will occur in larger numbers. Savannah sparrows, clay-colored sparrows, and vesper sparrows will occur under both heavy and light grazing conditions, usually in association with shrubs, but these species will not make up a dominant proportion of the passerine populations. Meadowlarks will apparently be equally common under both conditions." (p. 710)

Thus, effects of grazing most often depend upon its intensity and localization. High intensity grazing profoundly alters breeding avifaunas from the "natural" state, generally in the direction of decreased species numbers and "complexity." Where rangelands are fenced into "pastures," grazing may be intensified where cattle are confined and eliminated from the areas from which cattle are excluded. Fencing thus sharpens the differences between locally adjacent plant communities and thereby creates a local mosaic of avian communities of differing species composition and structure--the sorts of differences noted above. In unfenced rangelands subjected to moderate grazing pressure it is likely that grazing effects are much less concentrated in both space and time, and thus presumably avifaunas are less changed from the "native" condition. The critical studies comparing grazed and ungrazed habitats in open rangeland, however, are lacking.

Another effect of grazing has become apparent from the studies of Raitt and Pimm (1974) in desert grassland at the Jornada Site near Las Cruces, New Mexico. They have suggested that present grazing practices and fire management are promoting shrub invasion, and thus benefit shrub-inhabiting birds to the detriment of grassland species. Raitt and Pimm suggest that these southern rangelands are very important for overwintering migrants from more northern breeding grounds. If these land management practices do alter the availability of various habitat types, there may be major changes in the migratory patterns or population levels of grassland birds. If winter mortality plays an important role in the population dynamics of grassland birds, as Wiens (1974a) and Fretwell (1972) have suggested, this habitat compression, intensifying competition among grassland species, may have important consequences.

Effects of Agriculture (Cultivation)

As with grazing, agricultural cultivation of rangelands breaks the more or less continuously varying expanses of native habitats into local mosaics of differing habitat types. Cultivation, however, involves the added element of enforced vegetational replacement or substitution--man's introduction of monocultured crop types which frequently differ markedly from the native vegetation both floristically and structurally. Frequently those cultivated vegetation types least resembling native grasslands (e.g., corn) are those which are planted in vast unbroken fields, while the agricultural types bearing closest resemblance to natural habitats (e.g., fallow fields, pastures) occur in quite small patches interspersed among other agricultural types.

Agricultural cultivation thus represents a major modification of natural conditions, and it is not surprising that the avifaunal responses to these conditions are more apparent than those to grazing. Species numbers overall are not appreciably different from those in natural (tallgrass) prairies of the region (table 2), and many of the species characteristic of tallgrass habitats also occupy agricultural systems (table 1). There is considerable variation in the species composition of various agricultural types, however, and total breeding densities and standing crop biomass are substantially reduced from those characterizing tallgrass prairies. We should note, however, that the comparisons of tables 1 and 2 are biased, since we have considered only agricultural types roughly approximating native prairies (fallow fields, hayfields, pastures, etc.) and have excluded more extreme cultivations such as alfalfa, corn, wheat, etc. In many of these habitats, avian breeding density and biomass are quite low, and the species present are generally not those characteristic of true rangeland conditions (see Graber and Graber 1963).

In general, the avifaunas of "grassland-like" agricultural habitats are dominated by characteristic rangeland species, especially Grasshopper Sparrows, Savannah Sparrows, and Eastern Meadowlarks (table 2). There are two important influences on avifaunal composition, however, which are instructive in considering the effects of agriculture. First, the size of a block of more or less uniform habitat type is significant. Thus

the plots sampled by Mitchell (1961) in Minnesota ranged from 13 to 28 acres (5.3 to 11.3 ha) in size. In all of the early successional (= "grassland-like") stages, only one breeding species was recorded. Most of these plots were probably too small and/or too isolated within a mosaic of other agricultural types to support a full range of characteristic rangeland forms (e.g., meadowlarks). The area studied by Wiens (1969) in Wisconsin, on the other hand, was 80 acres (32.4 ha) and was bordered on most sides by fallow fields or pastures. Here a full complement of most of the "typical" tallgrass prairie forms occupied breeding territories. Thus reducing the size of habitat blocks through agricultural practices may of itself render areas unsuitable for occupancy by true rangeland bird species. The second factor is distance, or perhaps more properly the degree of continuity with true rangeland habitat types. Most of the rangeland bird species are wide-ranging, an adaptation to the inherent unpredictability of these habitats, especially in the Great Plains (Wiens 1974a, Owens and Myres 1973). There are limits, however, to the distance these species will disperse across unsuitable habitat (e.g., intensive agriculture or deciduous forests) to occupy small patches of suitable habitat. Thus Johnston and Odum (1956) recorded only Eastern Meadowlarks and Grasshopper Sparrows as breeding species in early field successional stages in the Georgia Piedmont; the absence of other "tallgrass" species may reflect the distance separating these Georgia fields from the main body of rangeland habitats (fig. 1).

Effects of Chemical Treatments

Avian populations exhibit some sensitivity to pesticides under a variety of conditions. Chlorinated hydrocarbons have received closest study, but currently on western rangelands insecticide treatments to control grasshoppers and other rangeland insect populations employ malathion and toxaphene (McEwen et al. 1972). What effects may these insecticide treatments have on rangeland bird populations? Two responses are possible: (1) direct effects, where birds are killed during or shortly after the treatment; and (2) more indirect effects, related to the loss of available food if the insecticide treatment removes substantial numbers of insect prey.

McEwen and Ells (in press) have investigated both effects in conjunction with the

IBP Grassland Biome. In northeastern Colorado two experimental areas were sprayed with toxaphene and malathion and compared with nearby control plots to study these effects. Information on the bird, small mammal, and insect populations, plant biomass, and rates of decomposition was obtained. Censuses show that populations of the most common species on the Colorado shortgrass prairie (Horned Lark, Lark Bunting, Western Meadowlark, and McCown's Longspur) did change in the toxaphene treated areas, but not in plots treated with malathion. The level of reduction in the toxaphene plots was estimated to be about 30% of control plot populations. Meadowlarks and nestlings of Horned Larks and McCown's Longspurs appeared to be especially susceptible to the toxaphene treatment. Adult Horned Larks were not susceptible in this study, although mortality has been noted in previous studies (McEwen et al. 1972).

One intriguing result of this study was an apparent depression of plant biomass on the treated areas. McEwen and Ells (in press) noted that on the control plots the total herbage biomass increased about 25%, but during the same growing season period total biomass on the malathion plots increased by only 10% to 11%, and on the toxaphene plots there was an increase of only 1.2% to 3.5%. There was a significant reduction in insect populations in all plots. The overall results of the experiment were thus somewhat puzzling, since it was expected that removal of the insects would result in an increase in plant biomass. The studies of Dyer and Bokhari (in prep.) indicate that insects may maintain or perhaps even stimulate plant production; removal of a portion of this component of the system, as by insecticide applications (or avian consumption) might thus produce "counterintuitive" feedback effects.

One other treatment deserves brief mention. Best (1972) analyzed the responses of Vesper and Brewer's Sparrows to controlled spraying (with 2,4-D) of sagebrush shrubsteppe in Montana. Spraying which produced a partial kill of sagebrush was not followed by significant change in the population densities of either species. At total kill levels, however, there was a 54% reduction in Brewer's Sparrow densities after spraying, a reflection of its greater dependence on shrub cover for nesting. Seeds represented a greater proportion of the diet of both species in sprayed and unsprayed areas, but in general the birds responded to the habitat changes following spraying by varying the relative quantities but not varieties of prey consumed.

The above analyses have been restricted to breeding bird communities in rangelands, but winter does come in these areas (often with a vengeance) and it merits consideration. We are hampered, however, by the nearly total lack of careful quantitative population studies conducted in rangelands at times other than the breeding season. This neglect is especially disturbing in view of the suggestions that population sizes of many rangeland species may be most severely limited by winter resource supplies (Wiens 1974a, Fretwell 1972), as Pulliam and Enders (1971) have demonstrated for wintering finches in southeastern "old field" habitats. Thus much of the structure of breeding avifaunas may be determined by events and resource relations during the winter (Raitt and Pimm 1974). Further, grassland or "old field" habitat types with their often substantial seed production may be major wintering habitats for populations of many species which occupy nonrangeland (e.g., shrub or forest-edge) habitat types during the breeding season (Johnston and Odum 1956, Wiens, unpubl.), especially in southern areas.

ENERGY FLOW

Consumer populations, such as birds, are most immediately linked to the ecosystem of which they are a part by energy flow. Our knowledge of the energetic relations of rangeland bird populations within these ecosystems is meager compared to the information available on breeding community composition, however. This of course stems from the present impossibility of directly measuring population energy flow of free-ranging birds under natural conditions, as well as from the preoccupation of avian ecologists over the past generation with measuring species compositions and breeding densities. Recent attempts to estimate the energetics of breeding populations or communities have utilized simulation modeling as an alternative to more direct studies (Wiens and Innis 1973, 1974). Our review of energy flow relations of rangeland bird populations draws from an application of this simulation model to information gathered on US/IBP Grassland Biome sites (fig. 1) from 1970-1973 (Wiens, in prep.).

Model Structure

The structure, logic, and assumptions of the simulation model employed in this analysis have been detailed elsewhere (Wiens and Innis

1973, 1974, Innis et al. 1974), and will not be reviewed here. The model is founded on the rationale that by combining information on various life history attributes of populations (e.g., clutch size, hatching success, population density), reproductive phenology, and individual bioenergetics (daily costs of existence metabolism, activity, egg production, and growth, modified to account for digestive efficiency), one may obtain valid estimates of the daily energy demands which individuals and populations (or assemblages of coexisting populations) place upon the ecosystem. In the analyses considered here, calculations were restricted to the breeding season (1 April-31 August), due to the paucity of information on wintering avifaunas.

Energy Flow Magnitudes and Patterns

Model analyses of energy flow are available for the breeding avifaunas of eight site-grazing treatment plots within the IBP Grassland Biome network. Among these plots, model estimations of the total energy demand of the breeding populations of all species present over the 150-day breeding "season" ranged from 0.89 kcal (ALE, 1972) to 2.92 kcal \cdot m⁻² \cdot season⁻¹ (Osage, 1971). Within this range there was substantial yearly and between-census variation at all plots (fig. 7). This variability of course is an indication of variation in the data inputs supplied to the model structure, primarily in values of population densities (as discussed above) and in ambient temperature regimes. Among the plots there were significant differences in mean total breeding season energy flow only between the Pantex grazed plot (which exhibited the greatest mean value) and the ALE and Pantex ungrazed plots. Again grazing intensity appears to be an important habitat influence, and we may examine this in greater detail by comparing different grazing treatments at the same site (table 6). Among the three sites available for comparison, only at Pantex was there a substantial difference between grazing treatments. This difference is surprising in view of the relatively high floristic and avifaunal similarity between the treatment plots at Pantex (Wiens 1973a), and reflects the marked differences in population densities of breeding species in the different treatments.

The model simulates energy demands on a daily basis so that daily as well as seasonal patterns of energy demand may be estimated. A closer analysis of the daily energy flow through the breeding season (Wiens, in prep.) shows that at the Cottonwood and Pawnee Sites the plots most strongly affected by grazing

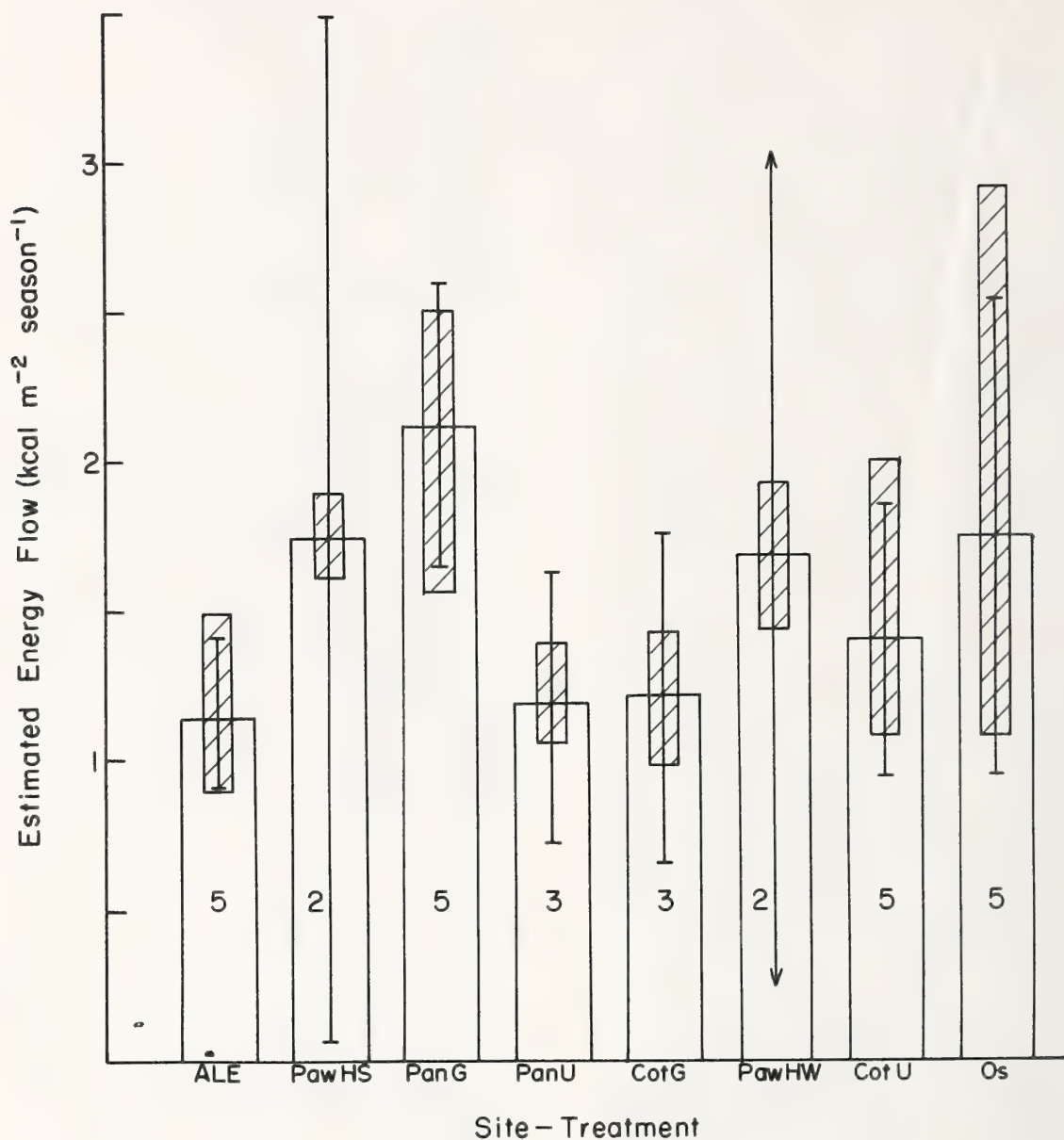


Figure 7. Estimated energy demand of breeding avifaunas at IBP Grassland Biome Sites, 1970-1973. Histograms indicate mean values, shaded boxes the range, and lines ± 2 standard errors of the means; numbers in histograms are sample sizes. Paw = Pawnee, Pan = Pantex, Cot = Cottonwood, Os = Osage, G = grazed, U = ungrazed, HS = heavy summer grazing, HW = heavy winter grazing. From Wiens (unpubl.).

Table 6.--Comparison of total seasonal energy flow
(kcal \cdot m⁻² \cdot season⁻¹) through breeding bird populations
on plots subjected to different grazing treatments at
the same study sites

Site	Grazed ^{1/}			Ungrazed ^{2/}		
	\bar{X}	S	N	\bar{X}	S	N
Pantex	2.12	0.381	5	1.18	0.185	3
Pawnee	1.75	0.195	2	1.68	0.347	2
Cottonwood	1.21	0.221	3	1.40	0.408	5

^{1/}Heavy summer at Pawnee

^{2/}Heavy winter at Pawnee

stress exhibited relatively little variation in daily energy flow over the breeding season while plots at those sites less directly influenced by grazing exhibited a progressive increase in daily energy demand from early May to a peak in late July. Daily energy demand of the bird populations at Pantex was also greatest in late July although the "peak" was less sharply defined and grazing treatments did not differ in the daily patterns of energy demand. The magnitude of peak energy demands was greatest at the Pantex grazed plot (0.019 kcal \cdot m⁻² \cdot day⁻¹), and least at the Cottonwood grazed and Pantex ungrazed plots (0.011 kcal \cdot m⁻² \cdot day⁻¹). In general, the overall similarities in energy flow patterns among the plots and sites were more impressive than the differences.

Another exercise using this simulation model may be instructive. Wiens and Innis (1973) utilized an activity budget subroutine of the BIRD model to estimate the effects of increasing grazing intensity on energy demands by Horned Lark populations. They projected a web of effects of increased grazing pressure (fig. 8); using realistic estimations of values for these effects, they predicted that increased grazing utilization by cattle might result in somewhat higher individual energy demands and substantially higher population energy demands in Horned Larks. Given information on food supplies and diets, the analysis could be extended. Thus Horned Larks occupying heavily grazed areas may require, on the average, nearly twice the number of prey individuals from their territory per hour of

time spent in foraging than individuals occupying ungrazed areas require. Viewed in another way, this suggests that when a Horned Lark is foraging in an ungrazed grassland, it must obtain one prey item every 10.4 seconds while in a grazed area the capture rate increases to one item every 9.0 seconds. If these values are considered in relation to the differences in territory sizes under different grazing regimes, the analysis projects that in ungrazed prairie, larks must obtain one item from each square meter of their territory every 27.5 hours of foraging time, and must completely search the territory once every 4.3 days; in grazed areas, the birds must capture one item per square meter every 16.4 hours of foraging, or must make one capture in each square meter of their territory every 2.9 days. Such values are, of course, only approximations, and the real situation would be influenced by many additional variables (not the least of which is the nonrandomness of prey distributions in time and space).

THE IMPORTANCE OF BIRDS IN RANGELAND ECOSYSTEMS

These patterns and magnitudes of energy flow tie bird populations to the functioning of rangeland ecosystems, but the more direct expression of this linkage is in consumption of food rather than transfer of kilocalories. We may thus view one dimension of the role or "importance" of birds in rangeland ecosystems through the patterns of food consumption.

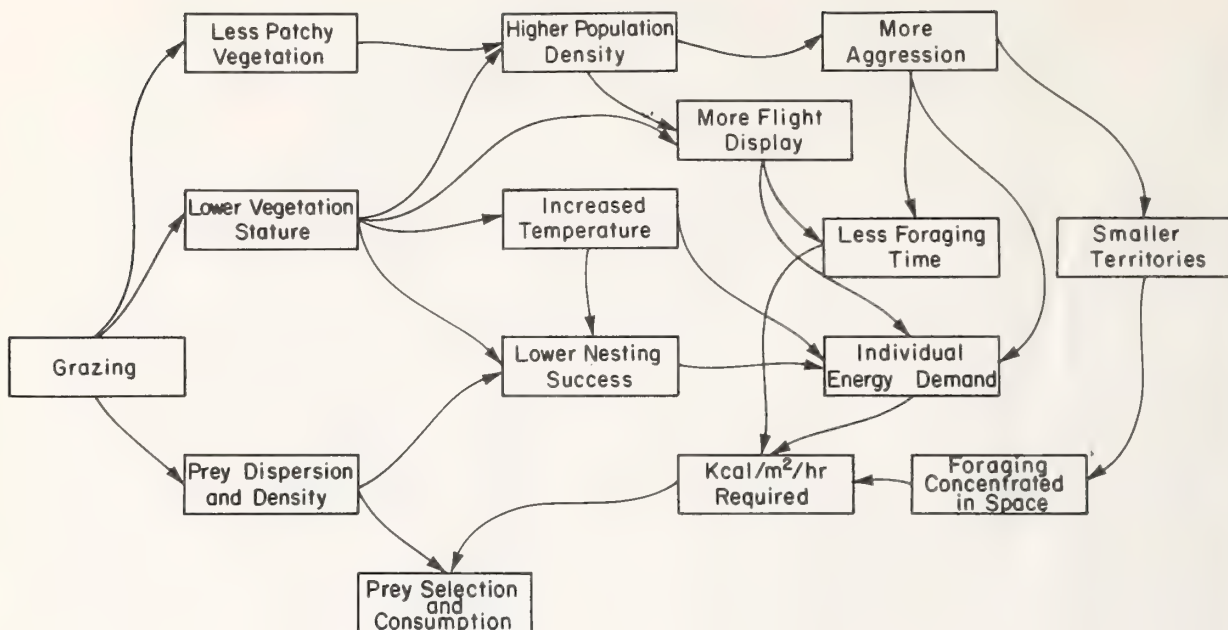


Figure 8. Conceptual representation of the effects of increasing grazing intensity on Horned Larks in grasslands.

Quantifying food consumption *rates* in natural situations is a difficult undertaking, however, and again we have relied upon the results of simulation model analyses to provide approximations of food consumption rates. The IBP Grassland Biome studies have gathered information on food habits of the dominant breeding bird species at several locations (Wiens et al. 1974, unpubl.). Knowing the approximate caloric value of prey items within each diet category, this information may be coupled with model projections of caloric demands to estimate prey consumption rates. Here we present only a very general treatment of these results.

The magnitudes of total consumption of plant and animal (invertebrate) prey categories by the total avian community over the 150-day breeding season considered in the model analysis are depicted in figure 9. Total prey consumption falls within a relatively restricted range for the six plots considered (0.215 to 0.405 g dry wt · m⁻² season⁻¹), and animal prey types rather consistently comprise roughly 80% of the total prey biomass consumed (except at the Palouse site, ALE, where seeds accounted for less than 5% of the breeding season food consumption). Given this dependency on

animal prey during the breeding season, it is appropriate to inquire how this consumption is distributed among various animal prey types. Rather than document such prey consumption in taxonomic categories, we have defined several "functional" categories of invertebrate prey. Thus "predaceous invertebrates" include spiders, some hemipterans, and carabids; "omnivorous invertebrates" are ants; "chewing plant-feeding" types are grasshoppers, weevils, etc.; "sucking plant-feeders" are leafhoppers and various hemipterans; "flower-feeding" forms include cantharid and anthicid beetles; and "scavengers" are insects such as scarab and tenebrionid beetles and flies. The documentation of the estimated consumption of these functional prey categories by the breeding avifauna during the breeding season is given in table 7. There is a fair degree of consistency in prey consumption patterns (the percentages contributed by the various categories) among the site-treatment samples, despite the variations in total amounts of prey consumed (fig. 9). Thus chewing insects dominate the diet in all samples, to the greatest extent at the ALE and Cottonwood ungrazed sites (74% and 68% of the total biomass consumed), less so at Pantex (36% and 44%). At Pantex predaceous invertebrates

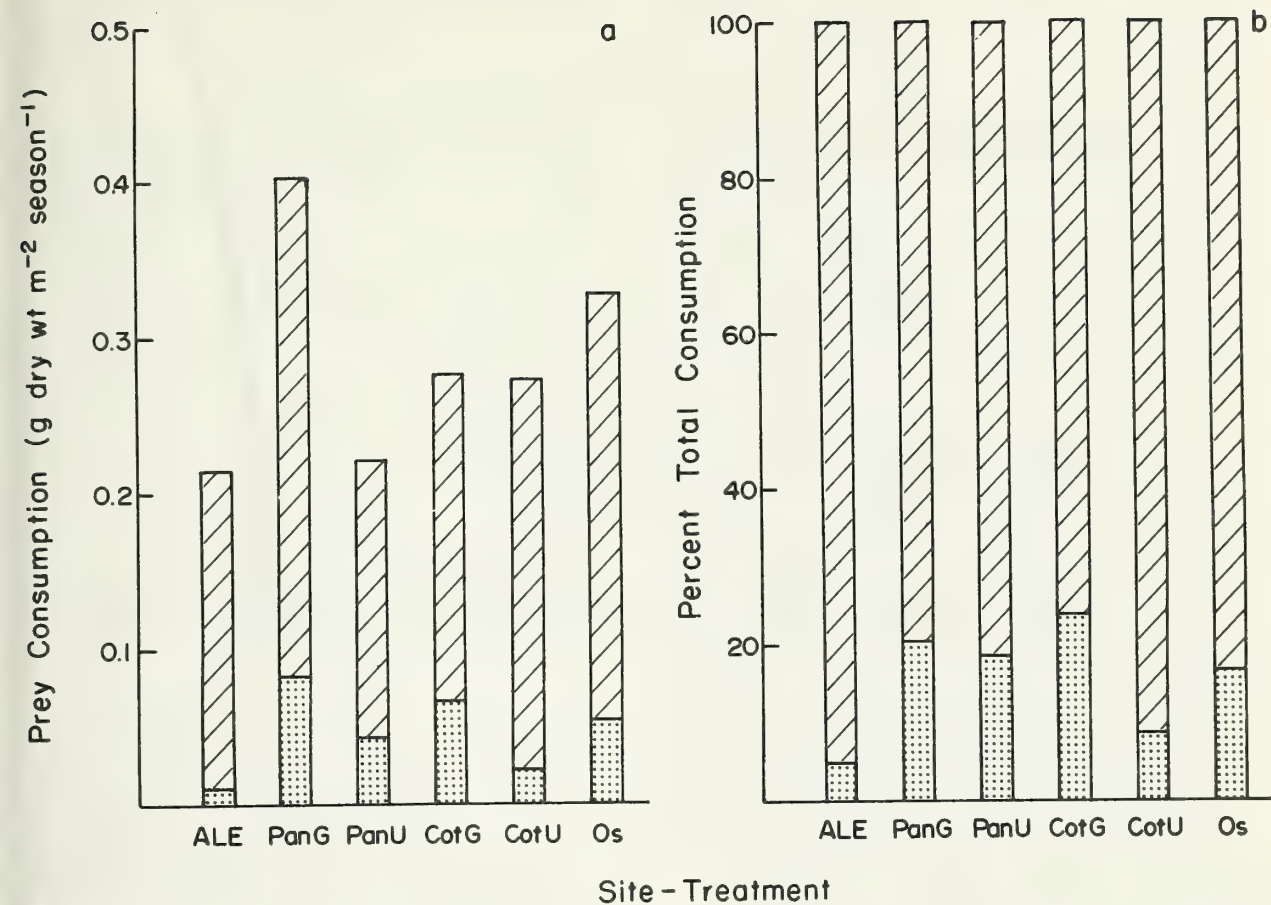


Figure 9. Patterns of prey consumption in breeding grassland avifaunas, estimated from simulation model output. A = prey consumption rates, B = composition of total prey consumption. Solid = seed prey, hatched = animal prey (primarily insects). Site and treatment codes as in figure 7.

Table 7.--Consumption of plant and animal prey categories (g dry wt \cdot m⁻²) during the breeding season by bird populations on IBP Grassland Biome sites. *Italicized values are percentages of total prey consumption (data from Wiens, in prep.)*

Site	Treatment	N	Invertebrate Prey Types							
			Plant Seeds		Preda- ceous	Omniv- orous	Plant-feeding			Scavenger
			Grass	Forb			Chewing	Sucking	Flower- feeding	
ALE	Ungrazed	5	0.0078 <i>3.6</i>	0.0020 <i>0.9</i>	0.0222 <i>10.3</i>	0.0111 <i>5.1</i>	0.1602 <i>74.2</i>	0.0030 <i>1.4</i>	0.0007 <i>0.3</i>	0.0089 <i>4.1</i>
Pantex	Grazed	5	0.0251 <i>6.6</i>	0.0446 <i>12.3</i>	0.0769 <i>20.3</i>	0.0273 <i>7.2</i>	0.1379 <i>36.5</i>	0.0474 <i>12.5</i>	0.0007 <i>0.2</i>	0.0183 <i>4.8</i>
	Ungrazed	3	0.0092 <i>4.8</i>	0.0199 <i>10.4</i>	0.0289 <i>15.0</i>	0.0136 <i>7.1</i>	0.0845 <i>44.0</i>	0.0204 <i>10.6</i>	0.0006 <i>0.3</i>	0.0151 <i>7.9</i>
Cottonwood	Grazed	3	0.0445 <i>16.6</i>	0.0191 <i>7.1</i>	0.0265 <i>9.9</i>	0.0199 <i>7.4</i>	0.1346 <i>50.1</i>	0.0044 <i>1.6</i>	0.0014 <i>0.5</i>	0.0181 <i>6.7</i>
	Ungrazed	5	0.0181 <i>7.0</i>	0.0014 <i>0.5</i>	0.0291 <i>11.2</i>	0.0169 <i>6.5</i>	0.1770 <i>68.3</i>	0.0043 <i>1.7</i>	0.0007 <i>0.3</i>	0.0116 <i>4.5</i>
Osage	Grazed	5	0.0572 <i>17.4</i>	0.0002 <i>t</i>	0.0713 <i>21.6</i>	0.0243 <i>7.4</i>	0.1572 <i>47.7</i>	0.0034 <i>1.0</i>	0.0001 <i>t</i>	0.0159 <i>4.8</i>

comprised 15% to 20% of the biomass consumption and at the Osage Site 22%, but elsewhere their contribution was less (10% to 11%). Omnivorous invertebrates consistently accounted for roughly 5% to 7% of the food intake, while scavengers contributed 4% to 8% of the diet among all sites. Sucking insects were important components of the diet only at Pantex, where they accounted for 11% to 12% of the biomass intake. Among the plant food component, grass seeds were a more important dietary component than forb seeds at all sites except Pantex.

Within an ecosystem context, these prey consumption patterns and magnitudes are important as they portray channels of energy flow and as they influence the dynamics of the prey populations, and thus prey inter-relationships with other system components. At our present stage of knowledge, it is impossible to determine with any precision the role that avian predation may play in controlling prey populations or their effects within the system (e.g., herbage consumption

by chewing insects or plant growth suppression by sucking forms). One approach to such determinations, however, is to compare the consumption amounts with the standing crop biomass of the various invertebrate groups present in the ecosystem. Unfortunately, appropriate data are not yet available from the IBP studies; a preliminary analysis, however, indicates no clear relationships between prey "choice" and prey standing crops. It is apparent, however, that one effect of insect consumption may have indirect consequences. Recent work by Dyer and Bokhari (in prep.) indicates that chewing insects (notably grasshoppers) could be extremely important in grassland ecosystems in regulating the ways that plants partition their energy reserves. Thus grasshoppers chewing on aboveground plant parts may stimulate the plants to translocate photosynthetic reserves into the crown and belowground parts. Such plants may be capable of faster regrowth once the insect feeding has been removed. Avian predation and "control" of insect populations may influence these

intertwined relationships, especially if the birds respond opportunistically to fluctuations in insect abundance. Such sensitive feedback relations may be of considerable importance in framing proper management strategies.

Another way of viewing the functional "importance" of bird populations in rangeland ecosystems is to evaluate the energy flow through the avifauna in relation to energy transfers among the various trophic components of the ecosystem as a whole. For example, the total plant biomass on the Pawnee National Grassland at the height of the avian breeding season was approximately 2,500 for 1970 and 1971 and approximately 1,600 g/m² in 1971 and 1972 whereas the total biomass of birds classified as primary consumers (seed-eaters) ranged from 6×10^{-4} g/m² in 1971 and 1972 to 9×10^{-4} g/m² in 1970. These comparisons are not direct, of course, since only a small portion of the plant biomass is potentially available to the birds as food. Nonetheless, it is apparent that avian biomass is several orders of magnitude less than that of primary producers. The biomass of the secondary consumers at the same time was also consistently low, on the order of 2×10^{-3} g/m².

There are, of course, other measures of "importance" of bird populations in rangeland ecosystems than energy processing or prey consumption, and ideally these also should be considered in habitat management assessments. Unfortunately, our knowledge of these other dimensions of importance is less precise or there are difficulties in making value judgments, so we can only just mention some additional considerations in determining "importance." First, in consuming prey organisms birds ingest not only energy but nutrients as well, and since population turnover is slow in birds, at least relative to invertebrate populations, these nutrients may be stored in the bodies of living birds for some time before being cycled to other components of the ecosystem. One permutation of this storage aspect is that these nutrients can be exported out of many North American grassland ecosystems over long periods of time, a mechanism made feasible by higher mortality rates on wintering grounds than on breeding grounds (Fretwell 1972, Wiens 1974a). For the most part, however, little attention has been given to the role of birds in ecosystem nutrient cycles. The most careful study is that of Sturges et al. (1974) in hardwood forests in New Hampshire. These studies suggested that bird populations

played extremely minor roles in the flux of nutrients into or out of the ecosystem or in nutrient storage. For example, the spring influx of migrants was estimated to introduce 3.4 g Ca/ha into the system, while the depature of young and adults in fall removed 6.4 g Ca/ha, a net annual loss of 3.0 g Ca/ha. By way of comparison, the net annual loss of Ca from this ecosystem via stream outflow is estimated at 9,430 g Ca/ha. Similarly, the total avian standing crops of Ca and P were estimated to be 6.0 g/ha and 4.3 g/ha respectively, while annual plant tissues contained 26,900 g Ca/ha and 2,700 g P/ha. These findings do not eliminate birds from a meaningful role in nutrient cycling in this or other ecosystems, but do suggest that any such role must be rather subtle.

Another dimension of importance is recreation, since birds, more than many animal groups, do possess aesthetic values to many people. Here especially the assignment of values is difficult. One might be able to count the numbers of man-days spent observing birds for enjoyment and translate this into some economic measure, and as dollars spent in the surrounding region. Ranchers in northeastern Colorado, for example, recognize "bird-watching" as an important use of rangelands, so long as these do not disrupt normal farming and ranching routines. As long as there are many people within segments of our society with much leisure time and with keen sensibilities about the quality of life, which includes avian species, the aesthetic values of rangeland species must be considered.

Finally, bird populations may be "important" if the populations exhibit such a restricted distribution and/or low abundance as to merit distinction as rare or endangered. As noted above, speciation rates in grasslands have been low, and few forms are locally endemic. Further, the wide-ranging habits of many of the dominant species (table 1) tend to thwart the development of circumstances which endanger the existence of species or definable populations. Locally, of course, rangeland species are sensitive to major habitat alterations (e.g., conversion to cultivation or extremely heavy grazing), and for species with somewhat restricted habitat affinities and/or distributional ranges (e.g., Mountain Plovers, Baird's Sparrows, McCown's Longspurs) such changes may be especially dangerous.

CONCLUSIONS

Our analysis of rangeland avifaunas has revealed several points which we believe are central to management practices. First, it is apparent that the breeding assemblages of many "native" rangelands are simple in structure and variable in total densities and avian biomass. This variability may represent a good deal of local or even regional redistribution of individuals on an annual basis, so that population "centers" continually move about. Coupled to these patterns is the relative stability of species composition of breeding avifaunas, reflecting the dominance of a few widely distributed, abundant, and apparently rather vagile species. On the one hand, the high degree of dominance by one or two species suggests that these avifaunas should be sensitive to disruption, since their structure depends on the status of these dominant forms. However, the observed fluctuations in densities and biomass and the wide distributions of dominant forms may produce a general "resiliency" in rangeland avifaunas, so that moderate habitat alterations (such as light to moderate grazing) produce only slight effects. More extreme habitat changes, such as heavy grazing or agricultural cultivations, may produce profound changes in all aspects of the avian communities, generally tending in the direction of increasing simplicity. Rangeland species may respond to such changes by shifting distributions to other, more suitable areas, but as intensive utilization of rangeland such as dryland farming or irrigation increases, the availability of suitable habitat for many bird species decreases. Because local avifaunas characteristically exhibit large-scale variations, it is difficult to use local census data as an "index" of population or community well-being, and major avifaunal shifts may be detected only after some "threshold" of habitat condition is passed. At that point, recovery of habitat quality may be an extremely slow process, given the long time scales of natural successional processes in many arid rangelands.

A second point, which follows from this, relates to the sorts of practices which might be followed to manage habitats for the benefit of nongame bird populations. Rangeland bird populations have evolved in association with large grazing mammals (e.g., bison), and thus moderate grazing pressures have only slight influences, and are in fact probably beneficial in creating small-scale environmental heterogeneity. Thus the major human

utilization of rangelands (grazing) is not incompatible with proper habitat management for nongame birds, at least if conducted at moderate intensity. However, the spatial scale of grazing, or of other habitat alterations, may have important effects. Large unbroken expanses of a single habitat type (i.e., ungrazed, lightly grazed) may support relatively similar breeding avifaunas, despite local variations in densities and biomass. As the size of areas of a given habitat type decreases and blocks of different habitats become interposed in a more reticulate mosaic, local variability in avifaunal composition ("beta diversity") increases. When habitat blocks become very small (perhaps 5 ha), however, communities may become increasingly simple, due to the disappearance of large-sized species which can no longer occupy full territories within a habitat type. Both of these trends are accentuated with increasing difference between interposed habitat types, up to a point. Thus breakage of uniform rangeland by blocks of agricultural cultivation reduces the size of available areas of suitable habitat, and increases the proportion of that area which is located in "edge" situations. Data are lacking, but it would seem likely that as boundaries between adjacent habitats become more distinct (i.e., the habitat types become more different), "native" rangeland species may exhibit an increasing tendency to shun edge areas. In other words, proper habitat management for rangeland nongame species should avoid substitution of extreme habitat types, such as cultivation or heavy grazing, for "native" rangeland conditions, and should retain habitat blocks of moderate size (e.g., perhaps 1 to 2 km² minimum).

Finally, we would like to draw attention to two aspects of the biology of rangeland bird populations which we believe merit close attention in future research. Most critical is a better knowledge of the dynamics and interrelations of wintering populations. If population size is strongly influenced by winter mortality (Fretwell 1972), then the status of given breeding populations may be determined to a considerable extent by influences elsewhere in the species' range. Thus, the variability in densities of breeding populations may reflect influences of wintering losses as well as yearly variations in breeding distributions. Further, habitat alterations (e.g., massive cultivation) in wintering areas will have confounding effects on attempts to manage breeding habitat for nongame species. Management must therefore

be framed on local habitat patterns in breeding areas as well as regional relationships of breeding and wintering areas. The interconnections of such areas are difficult to determine but critical. The lack of much information on wintering dynamics must lead us to be extremely cautious in forming management policies, especially in the southern rangelands in which winter utilization by birds is great (Emlen 1972).

The second area in which we see a need for intensive research is the documentation of the interrelationships between avian predators and their prey populations. Measurements to date have been of a static nature, detailing diet composition and perhaps prey resource abundance (= standing crops) at various points in time. What is needed is a dynamic approach, which considers the functional processes linking consumers to their prey, and from this determining the true effects of predation on ecosystem structure and function. There is enough information available to suggest that these effects may not always be straightforward. Since management policies should be founded upon a perspective for the total system which encompasses the "target" organisms (in this case, nongame birds), such information is essential.

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APPENDIX I

Representative studies of the ecology of characteristic rangeland bird species.

Species	Authors
Dickcissel	Emlen and Wiens 1965, Wiens and Emlen 1966, Schartz and Zimmerman 1971, Zimmerman 1971, Sealy 1971
Henslow's Sparrow	Hyde 1939, Robins 1971a, 1971b
Meadowlarks	Lanyon 1956a, 1956b, 1957, 1962, 1966, Rohwer 1972, Szijj 1963, 1966, Roseberry and Klimstra 1970, Platt 1963
Grasshopper Sparrow	Smith 1959, 1963, Wiens 1973b
Bobolink	Martin 1971, 1974, Tester and Marshall 1961
Baird's Sparrow	Cartwright et al. 1937
Savannah Sparrow	Wiens 1973b
Vesper Sparrow	Evans 1964
Field Sparrow	Evans 1964
Chipping Sparrow	Evans 1964
LeConte's Sparrow	Murray 1969
Sharp-tailed Sparrow	Murray 1969
McCown's Longspur	Felske 1971, Creighton 1974
Lark Bunting	Creighton 1974
Horned Lark	Pickwell 1931, Niles 1973, Trost 1972, Creighton 1974
Mountain Plover	Graul 1974

Range Management Practices and Bird Habitat Values¹

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Abstract.--This paper aggregates available information on the known and probable effects of fourteen range management practices upon nongame bird habitat. Five research goals are suggested to secure the additional information necessary to predict these effects, to determine bird habitat requirements, and to present findings in a manner usable in the formulation of range management plans.

Within the various rangeland habitats from sea level to above timberline, many management practices are available for increasing grazing capacity, improving range condition, making more efficient use of existing range, and creating new range. All are designed to favor livestock. On lands managed by agencies of the Federal Government, the anticipated effects of these practices are evaluated and reported through the environmental impact statement process. As part of the fauna of any rangeland habitat, nongame birds receive consideration along with big game, upland game birds, etc. An examination of nearly any environmental analysis report or impact statement will show, however, that the section on "birds," "other birds," or "nongame birds" is short, speaks in generalities, and is almost useless for evaluating any effects on birds and their habitats.

Although many range managers give little or no thought to nongame wildlife and its habitat requirements, the number who do, or would like to, is growing. Range managers are becoming aware of the value of rangeland habitat for animals other than cattle and sheep. In spite of this new awareness and interest, very little information is available about the habitat requirements of birds in rangeland habitats, and even less has been published about the effects of the various management practices.

Hilden (1965) and Svardson (1949) have reported that birds select their habitats by a reaction that is triggered by the summation of certain environmental stimuli, and that if these stimuli fail to reach a threshold level, internal motivation, probably associated with hormonal action, lowers the threshold to a point where the existing external stimuli will often trigger a response. The triggering stimuli need not be essential for the survival of the species, and Hilden (1965) speculated that they involve landscape; terrain; nest, song, lookout, feeding, and drinking sites; other animals; and food.

It may be said that birds associate certain habitat characteristics with "home," and any management activity that alters these characteristics to the point that they fail to trigger the habitat selection reaction is detrimental to the affected species of birds. We here examine some range management practices and point out what is known and what needs to be learned about their impacts on nongame bird habitat.

LIVESTOCK GRAZING

Overmire (1963), in a northcentral Oklahoma study, found that populations of dickcissels and Bell's vireos were 50 percent lower on grazed than ungrazed lands. He felt that grazing reduced the number of suitable nesting sites. Smith (1940), in another Oklahoma study, found that in the mixed-grass prairie, birds quickly disappeared from overgrazed lands. However, as shown by Weatherill and Keith (1969), grazing by domestic livestock is not necessarily in itself unacceptably detrimental to bird habitat. Moderate grazing may improve habitat in some cases, for species such as the mountain plover and meadowlark.

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Owens and Myres (1973), in a southern Alberta study, found that disturbance of a fescue grassland by mowing or cattle grazing reduced or eliminated the populations of Baird's sparrow and Sprague's pipit, did not affect the population of savannah and clay-colored sparrows and western meadowlarks, and permitted the ingress of horned larks and chestnut-collared longspurs.

Dambach and Good (1940) found in an Ohio study that protected woods supported more than twice the bird population—both in individuals and species—than did grazed woods. They also noted that 50 percent of the species found in the grazed woods were hole-nesters as compared to 31 percent in the protected woods. None of the species in the grazed woods nested on the ground, and only one, the indigo bunting, nested in herbaceous or shrubby cover. Although these findings differ from those of Weatherill and Keith (1969), in an Alberta study, grazing intensity in the Ohio study was more than three times higher than the heaviest intensity in the Alberta study. Weatherill and Keith found that numbers of white-throated sparrows, ovenbirds, least flycatchers, and red-eyed vireos were not affected by either light or heavy grazing in an aspen forest, even though white-throated sparrows and ovenbirds are ground nesters.

GRAZING SYSTEMS

More important than whether an area is grazed is how, when, and to what extent it is grazed. Many grazing systems have been used over the years to either maximize livestock gains, use the forage at the best time, provide rest for the plants during all or part of the growing season, or to defer use until seeds have matured. Grazing systems in use include yearlong, continuous, deferred, deferred rotation, rest rotation, common use, and alternate use by kind of livestock (Society for Range Management 1964).

Yearlong Grazing

From the bird habitat standpoint, yearlong grazing is probably the most detrimental of the grazing systems because understory, and in some cases midstory, vegetation is never allowed to rest. Unless the range is very lightly stocked the amount of vegetation present is likely to be insufficient to provide adequate food and cover for seed-eating birds that nest on or near the ground. Also, if grazing has been heavy enough, habitat characteristics may have been altered enough that the habitat-selection mechanisms of the normal nesting species will not be triggered.

Continuous Grazing

Although yearlong grazing is continuous grazing, not

all continuous grazing is yearlong. It may be just for the grazing season. Since grazing seasons may be winter, spring-fall, or summer, continuous grazing may or may not be detrimental to bird habitat, depending upon the season of use and the stocking rate. If seasons of use were to be ranked according to the degree of detriment to bird habitat, continuous summer use probably would rank first because it occurs during the nesting season of most birds. This would be followed by spring, fall, and winter use.

Deferred Grazing

Deferred grazing, which is the discontinuance of grazing on an area for a specified time (usually until seed maturity) during the growing season, is probably less detrimental to bird habitat than either yearlong or continuous grazing. The period of deferment usually coincides with the nesting season, and ungrazed vegetation is available for concealing nests. Roseberry and Klimstra (1970) found that the extent of overhead concealment of nests controlled the nesting success of eastern meadowlarks.

Deferred Rotation and Rest Rotation Grazing

Deferred rotation and rest rotation systems may be looked upon with mixed emotions from the bird habitat standpoint. Nearly always, when a pasture is deferred or rested, another pasture absorbs the grazing pressure during the period of deferment or rest. Any benefit to bird habitat on the deferred or rested pasture is likely to be offset by heavy use of the grazed pasture. This heavy use may not only reduce food and cover, but also may affect the productivity of ground-nesting birds through the trampling of nests.

Common Use Grazing

Common use—the use of range by more than one kind of animal, either at the same time or at different times within the same growing season—is probably as bad or worse for bird habitat than continuous or yearlong grazing because more kinds of vegetation are utilized. Since cattle and horses prefer grasses and grass-like plants, sheep prefer forbs, and goats prefer shrubs, the advantage of this grazing system to the livestock owner is based on more complete utilization of the vegetation. Common use may be an advantage to stockmen, but because bird diversity increases with the number of strata in the vegetation and with the evenness of foliage apportionment among the strata (MacArthur and MacArthur 1961, Tramer 1969, MacArthur 1964), it is quite possibly a distinct disadvantage to birds.

Alternate Use Grazing

Alternate use by kind of livestock is the use of range by more than one kind of animal (usually cattle and sheep), but in different years. Use by one kind of animal may continue for several years before the use is alternated. This system is sometimes used to improve cattle range that has deteriorated to the point where the vegetative cover is largely forbs. It may be less detrimental to bird habitat than common use because at least one kind of vegetation is not being significantly utilized during a grazing season. The cover and food plants left unutilized may or may not meet the requirements of the birds normally found in that habitat.

Although no specific grazing system was mentioned, Monson (1941) in an Arizona study, reported that when a severely deteriorated range was placed under proper grazing management and water spreading dams installed, the result was a greater than 100 percent increase in the small bird population. How much of the increase can be attributed to grazing management and how much to water spreading was not determined, but the study dramatically illustrated the importance of good range management to bird habitat.

Good bird habitat management may also be important to good range condition. In New Zealand, it is suspected that range deterioration has reduced populations of native birds and allowed the increase of insects that damage the residual grass (Daubenmire and Daubenmire 1968).

Basic studies of the habitat requirements of different species of birds would provide the data necessary to evaluate the effects of different grazing systems and range deterioration in general.

RANGE IMPROVEMENTS

Any structure, excavation, or treatment to facilitate management of range or livestock is termed a range improvement.

Structural Improvements

The most common structural improvements are fences and the structures built as part of water development such as windmills, troughs, and trick tanks. Fences probably have little or no detrimental effect on bird habitat, and may in fact improve it by providing hunting perches for raptors, flycatchers, and shrikes, and safer resting areas for other birds, particularly where shrubs have been removed from surrounding country. The same would be true for windmills and trick tanks when considered separately from the water with which they are associated. Troughs are a little different in that

they can constitute a death trap for birds and small mammals unless effective escape ramps are provided.

Water Development

Water developments such as springs, ponds, trick tanks, and wells, which increase the amount of water available or provide it where none was before, are beneficial to bird habitat in some ways and detrimental in others. One detrimental effect might be that the water-providing value of a pond could be more than offset by the inundation of the original habitat, although this seems unlikely unless the pond is very large, or the original habitat was extremely critical to a particular bird species. Another detrimental effect could be that the development of water could attract predatory mammals and snakes to the extent that ground-nesting birds would not be able to reproduce.

Probably the most detrimental effect of water development of any kind is the overuse and resulting deterioration of the area in the vicinity of the water. The regular coming and going of livestock is not as detrimental as the damage to vegetation and soil caused by the reluctance of livestock to leave the area, especially during the hotter part of the day. The vicinity of the water development becomes a loafing area for livestock where ground cover and bird nesting habitat are destroyed and trees are damaged or destroyed by rubbing, browsing, and trampling.

Possible beneficial effects, besides the increased availability of water, might be an increase in insects attracted by the water, livestock, and manure, creation of dusting areas, and in the case of ponds, creation of new habitat in the form of water, mudflats, or marsh.

Herbicidal Treatment

Herbicides are used to kill a variety of plants, mostly woody, so they can be replaced with species useful as livestock forage. The most common herbicide used is probably 2,4-D. Outside of studies of the effects of 2,4-D on sage grouse habitat, there seems to have been little study of the effects of herbicidal treatment on bird habitat.

Available information comes from a central Montana study by Best (1972), on the effects of herbicidal control of sagebrush on Brewer's and vesper sparrows. Only on total-kill spray plots did breeding pairs of Brewer's sparrows decline after spraying, but this decline was greater than 50 percent. Pairs of vesper sparrows did not change significantly. Although both species utilized sagebrush for nesting cover, vesper sparrows nested on the ground, whereas Brewer's sparrows nested in shrubs. The Brewer's sparrow selected larger sagebrush for nest



(Photo by Max Schroeder, USD1)

The Brewer's sparrow is virtually eliminated by sagebrush eradication.

sites when the shrub was dead, but spraying apparently did not influence shrub size selected by the vesper sparrow. The Brewer's sparrow compensated for lack of foliage by selecting more densely branched sagebrush. Additional concealment by grass was greater at nest sites of both species when the shrub was dead.

Plant foods (primarily grass seeds) represented a greater portion of the diets of both sparrows on the sprayed area, while animal foods decreased. As a result of spraying, major plant and animal foods consumed differed in amount rather than in variety. The author concluded that the major factor in determining the ultimate effect of sagebrush control on Brewer's and vesper sparrows would be dependence upon sagebrush for nest cover. Five years after treatment, Pyrah and Jorgensen (1974) found that the Brewer's sparrow was virtually eliminated from the total-kill plot, the only treatment resulting in measurable adverse effects on nongame bird populations in the study area.

Rangeland Seeding

Many thousands of acres of depleted and burned rangeland are seeded each year to improve range condition, increase livestock production, and prevent erosion. Grasses predominate in most seeding mixtures, but legumes are sometimes included. Rangeland seeding,

particularly with native species, is largely beneficial to bird habitat because it quickly changes the vegetation from some stage of succession to one more nearly resembling climax, thus providing food and cover better suited for the normal bird species and populations found in an undisturbed ecosystem.

The ecological distribution of birds is controlled by life form rather than species composition of the vegetation (Pitelka 1941, Odum 1945, Johnsgard and Rickard 1957, Pettingill 1970). After seeding, numbers and species of birds filling niches provided by subclimax range conditions are displaced. Although seeding with native species provides better habitat for bird species associated with near-climax vegetation, the benefits may be offset by the effects of heavier grazing resulting from increased forage production. Rangeland seeding, as with all man-made and natural changes, is neither all good nor all bad.

Type Conversion

Vegetative type conversion usually involves the removal of shrubs and small trees to favor increased forage production by herbaceous plants, usually grasses. Types can be converted by a variety of methods such as chaining, dozing, raiing, rootplowing, and burning. Conversion may or may not be followed by seeding,

depending upon the composition and density of the herbaceous understory and the amount of soil disturbance caused by the operation.

Type conversion can be beneficial or detrimental to bird habitat, depending upon the extent, pattern, availability, and stage of maturity of the type, its successional stage in the climax community, and whether it provides for specialized habitat requirements of certain bird species. Probably no other practice provides such abrupt changes between vegetative types as type conversion. These abrupt changes produce what is well known to wildlife biologists as "edge effect." The most diverse and dense bird populations are often found in the ecotone of two contrasting vegetation types (Lay 1938, Johnston and Odum 1956, Johnston 1947).

In an Arizona study to determine whether chaparral clearance by rootplowing affects the overall species diversity and population densities of birds and mammals, Loe and White (1974) concluded that if treated areas are well planned, kept relatively small and broken up, and are reseeded with additional herbaceous species, the results are increased vegetative diversity and faunal productivity. The only bird species adversely affected to a significant degree was the common bushtit, which prefers rather dense vegetation.

An example of the detrimental effects of poorly planned type conversion on a single bird species is the removal of Ashe juniper on the golden-cheeked warbler on the Edwards Plateau of Texas. The golden-cheeked warbler requires mature Ashe juniper for nesting. Second-growth stands do not provide the habitat requirements. Removal of this tree for range improvement and expanding urbanization is responsible for the decline of the golden-cheeked warbler to the extent that it is included on the list of threatened species published by the Bureau of Sport Fisheries and Wildlife (1973).

Daubenmire and Daubenmire (1968) state that many birds require woody plants as nesting or perching sites, and that the eradication of sagebrush eliminates certain bird species which while rearing their young, normally make heavy use of insects. Eliminating these birds from the community removes an important insect control.

Fire Management

Fire as a range management tool is used mainly in the oak-woodland and chaparral vegetation types in California, but has also gained acceptance in the Ozarks and the Southeast. The use of fire in the chaparral type usually amounts to type conversion, and from the bird habitat standpoint has many of the same effects.

Bird species found in the chaparral are completely displaced by a large, clean burn, and are replaced by species found in open country. This change continues for only a few years unless the type conversion is maintained by controlling the sprouts of the native vegetation.

However, small irregular areas of chaparral type conversion, or large areas having brush islands followed by seeding of adapted grasses and forbs, can increase the "edge effect" and thereby the diversity of bird species. Bell and Studinski (1972), in a study of habitat manipulation and its relationship to bird populations on the Cleveland National Forest in southern California, found that the largest populations and greatest species diversity were in the oak-woodland type, which contained 28 species, and decreased in the following order: type conversion with brush islands-18 species, burned chaparral-11 species, type conversion without brush islands-8 species, and mature chaparral-7 species.

The use of fire in the oak-woodland type and in the Southeast does not usually result in type conversion unless the fire is unusually hot and burns as a crown fire. The purpose of this type of burning is usually to reduce what is considered to be excess vegetation in the shrub and herbaceous strata to promote free movement of livestock and production of forage. Fire used in this way can achieve the desired results, and can prevent the occurrence of conflagrations caused by excessive fuel buildup. However, it can also have a pronounced effect upon the diversity of bird species that normally nest in the lower and middle vegetation strata of the woodland type. According to Lack (1933), Beecher (1942), Oelke (1966), and MacArthur (1964), the selection of breeding habitat by woodland birds is based on the recognition of foliage patterns and density which fit preconceived notions of "home." Removal or modification of any of the vegetative strata, whether by burning or heavy grazing, reduces the diversity of bird species found. Dambach (1944), in a study of adjoining grazed and ungrazed woodlands, found the average breeding bird population in ungrazed woodlands included 11 species as compared to only 4 species in heavily grazed woodlands.

Rodent Control

Rodent control to reduce competition for forage is a fairly common practice. Black-tailed prairie dogs, ground squirrels, and pocket gophers are the most common target species. Poisoned grain is usually the method used for control. Considerable research has been done on the relationship of rodent control to forage production and range condition, but apparently none has been done on its relationship to bird habitat.

Although it is well known that prairie dog poisoning

affects burrowing owls by destroying their preferred habitat, the most apparent effects of rodent control are direct effects on the birds themselves rather than their habitat. Some primary poisoning of birds occurs when they consume poisoned bait, and there is probably some secondary poisoning when poisoned rodent carcasses are eaten by carrion-eating birds such as magpies, crows, ravens, and vultures. Secondary poisoning could also occur if raptors eat poisoned, but still-living rodents, but this probably is not common because most rodents, when poisoned, return to their burrows to die.

RESEARCH NEEDS

We have examined various range management practices in light of what is known about their impacts on bird habitat. It is apparent that these practices bring about great changes in both the plant and bird components of rangeland ecosystems. These changes are likely to become even more pronounced because of the increasing emphasis on grass-fed beef to meet the demands for red meat. If the land manager is to make sound range management decisions which provide for the other uses and values of rangeland ecosystems, he must be able to predict the effects of these changes. From the nongame bird habitat standpoint, the following appear to be logical research goals:

1. Identify the bird species which are under the most stress from range management practices.
2. Quantify the habitat requirements of these species (food, water, nesting, density, composition and arrangement of vegetation) in such a manner as to be useful in formulating range management plans.
3. Determine which range management practices have the greatest impact on the habitats of these birds, and the tolerances for each species and practice.
4. Determine how range management practices and existing plant communities can be manipulated to strike a balance to benefit both humans and birds.
5. Determine, quantitatively if possible, the ecological, esthetic, and economic consequences of losing these bird species in the various ecosystems.

Until these goals are achieved, bird habitat values cannot receive adequate consideration in range management planning.

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Raptors in Range Habitat¹

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Abstract.--A discussion of the diverse goals of raptor management, an evaluation of present, past, and future human impacts on wild raptor populations, and suggestions for positive conservation measures for raptors in range habitat.

GOALS OF RAPTOR MANAGEMENT

Historically, western man has tended to view raptors mainly as predators of game and livestock. Until recent years even many naturalists tended to consider birds of prey more as enemies of favored species than as favored species in their own right. However, in the last few decades, especially following the excesses of the DDT era in this country, considerable positive interest in raptors has developed in nature enthusiasts, biologists, and conservationists. In addition, there has been a growing interest in raptors from the sport viewpoint, and falconers have become a well-organized, if still relatively small, special interest group. These newer viewpoints on raptors are not all harmonious with one another, nor are they compatible with older viewpoints which persist.

The endangered species act of 1973, along with other federal and state regulations, firmly commits us to the concept of raptor conservation. Beyond this basic idea there is as yet no consensus as to what goals, if any, are to be striven for regarding raptors. Although a number of proposals have been advanced for methods of increasing endangered and non-endangered populations of wild raptors, "for example those of Olendorff and Stoddart (1974)", the end-points have generally been left unclear. One senses

from some papers that it is assumed that maximal numbers of raptors are the desired goal, and that whatever means work toward this goal should be encouraged. Others may disagree with this goal. For example, to many wildlife enthusiasts raptors are uniquely important in representing the spirit of wilderness, and to the extent that maximal populations are achieved by "domesticating" raptors to artificial nesting structures, etc., such values are harmed.

The question of goals in raptor management is not a simple one. We distinguish three major points of view on raptors which should be considered in management decisions: economic, recreational, and scientific. These points of view are not all mutually exclusive, nor are they homogeneous, nor all-inclusive, but they serve to help point up some of the conflicts that exist concerning goals of raptor management.

Economic considerations tend to be important considerations in our culture, and raptors have economic importance in a number of ways, some clearly perceived, others much less clear. It is likely that in a broad sense raptors are beneficial to man's economic well-being by helping to maintain stability and diversity of natural ecosystems (see Craighead and Craighead 1956, Paine 1966), but such benefits are very hard to measure and balance against the direct losses experienced by the sheep rancher or poultry farmer, and it is optimistic to assume that such broad views, even if appreciated, will have much impact on day to day affairs of these interests. Eagles do kill lambs on occasion, peregrines do eat waterfowl, Cooper's hawks do take poultry at times, and goshawks do eat game birds. It is not surprising that the interests perceiving themselves negatively affected by such predation have attempted to counter the threat by a general policy of harassment and slaughter of raptors.

Raptor control measures have not always been economically sound, that is, more has sometimes been invested in the destruction of raptors than losses apparently justify,

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and one suspects that often more than economics is involved in the process. The killing of raptors that used to occur at Hawk Mountain, Pennsylvania was probably motivated more by sport than by economics. In fact, there was never any attempt here to compare costs and benefits, something one might expect if strict economics were the only consideration. Likewise, it has never been shown that the broad program of slaughter of eagles from airplanes that was practiced in a number of western states really paid in terms of savings in sheep and goats being greater than the expense of running the control operations (see reviews in Snow 1973a, Kalmbach *et. al.* 1964, Packard *et. al.* 1969). Such economic gains or losses, to be sure, are extremely difficult to compute, especially if one attempts to take into account indirect benefits of eagles, such as their predation on small mammals competing with livestock for forage, and if one attempts to take into account the uncertainties in distinguishing eagle kills from lambs eaten as carrion by eagles. Newton (1970) reviews studies which show that the economic benefits of control of predators of game birds are often, perhaps generally, less than the costs of the control. He emphasizes that for game birds a much greater return on investment can be expected if monies are devoted to habitat improvement rather than to predator control. Thus while programs of raptor control are often rationalized as economic necessities, and may be perceived as such, the true economics of the control programs are often poorly understood.

The economic impacts of raptors are more diverse than their effects on game and livestock. For example, the conflicts that have developed in California between proponents of preservation of the condor and mining and dam-building interests have been severe (see Sibley 1969). Similarly, the saving of the everglade kite in Florida is going to mean that water supplies and enough habitat will have to be guaranteed. The severe competition for water and land in this state can only mean that some interests will have to face economic restrictions if the kites are to be saved. Such habitat-related conflicts of interest can be expected to increase in the years ahead.

On the positive side, peregrines have been used with great success in clearing airport runways of birds (for an economic benefit of \$600,000 in one year at one airport - see Kuhring 1969), some falconers actually do procure food with their birds, and a great deal of money is spent by bird watchers anxious to view raptors. The beneficial economic impact of Hawk Mountain on local communities must be considerable. In a broad and hard-to-measure sense the reductions in populations of pest mammals and insects produced by raptors may be of significant importance to agriculture, especially to agriculture of the future which may be less dependent on chemical

control methods. Everglade kites in Guyana are valued because of their predation on snails feeding on young rice shoots.

Overall it is very difficult to generalize about the economic impacts of raptors. While we would argue that strong or even maximal raptor populations are probably of transcendent economic benefit to man, we can probably assume that there will always be segments of the population who will on economic grounds seek a goal of minimal numbers of at least certain species.

The recreational viewpoint of raptors is likewise not homogeneous. For many nature enthusiasts the opportunity to enjoy native raptors in natural or close-to-natural settings is an important part of the experience of wildlife. The thousands of people gathering annually at migration points such as Hawk Mountain testify to a keen recreational interest in these birds. Many enthusiasts react negatively to birds held in captivity, as for falconry, and desire their raptor experiences to be as little tainted by management as possible. To such people the sight of a golden eagle nesting atop a man-made tower does not compare to the sight of one at a cliff-side eyrie. For them the maximizing of raptor numbers is a goal secondary to keeping them in as wild a condition as possible.

For falconers, a primary goal may well be maximizing numbers of certain species available in the wild. Falconers tend to favor the larger falcons, accipiters, and certain buteos. To some extent this favoritism may work to the detriment of other raptor species. For example, it is possible to imagine pressures developing from falconers for control of horned owls in the vicinity of falcon eyries. There are those who suggest that captive breeding of raptors may someday supply all the raptors needed for the sport, and certainly great strides have been made in breeding some of the more difficult species, such as peregrines, in recent years. However, this argument ignores the fact that wild-caught birds, especially those that have reached independence in the wild, generally make superior hunters for the sport. It is questionable that this aspect will change through improved captive-rearing techniques, and it is questionable that all falconers will be satisfied with captive-reared birds. As we will discuss later in this paper, there can be little doubt that falconry presently represents predation on wild raptor populations. So long as wild populations remain the major source of birds for the sport, there will be potential conflicts with other positive values represented by raptors.

Finally, from the point of view of biologists goals again may be diverse. For many, the primary goal of raptor conservation may be to preserve diversity in the wild rather than to achieve maximal numbers, for it is through studies of raptors in a variety of settings that insights into ecological and evolutionary phenomena are

to be gained. Too-intensive management may be detrimental. Biologists need control animals as well as experimental.

There is no way that diverse goals such as the ones mentioned above can all be optimized simultaneously, and solutions to conflicts of interests will have to be sought either in the sense of setting aside different regions for different primary purposes, or in the sense of trying to find the best compromise for given regions.

In the rest of this paper we discuss the more important human impacts on raptor populations and some positive management methods for manipulating and sustaining wild raptor populations. Since range habitat in the broad sense of areas used for grazing includes everything from swamplands to deciduous and coniferous forests, and since raptors are not being covered specifically in the other symposium sections, we will keep our discussion fairly general. For our purposes here raptors are defined as members of the falconiformes and strigiformes.

HUMAN IMPACTS ON RAPTOR POPULATIONS

Habitat Considerations

As a group, raptors occupy virtually all terrestrial, fresh-water, and coastal-marine habitat types that are productive enough to sustain reasonable populations of small vertebrates and invertebrates. As individual species, raptors vary from habitat specialists like the osprey, which is limited to bodies of water with strong fish populations, to habitat generalists like the red-tailed hawk, which can be found in habitats ranging from the dense tropical rainforests of Puerto Rico to the deserts of Arizona to the taiga of Alaska. By in large it is the specialists which are most vulnerable to habitat loss or change, yet even with the massive alterations of the landscape produced by man in North America we have yet to see the extinction of any species of raptor. To be sure, a number are currently classified as endangered: the California condor, the everglade kite, the Hawaiian hawk, the southern bald eagle, and two races of the peregrine falcon, anatum and tundrius. Still others are candidates for threatened status, although an official federal list of threatened species has yet to be drawn up. In addition, there are a number of raptors which reach the U.S. only along its southern border: short-tailed hawk, white-tailed hawk, zone-tailed hawk, gray hawk, black hawk, ferruginous owl, caracara, and aplomado falcon. While not in danger of extinction at the present time in the parts of their ranges below the Mexican border, these species are all rare in the U.S. and deserve special attention if they are to remain a part of our avifauna. To some extent all of the above

species have been affected negatively by habitat loss and change.

The major habitat changes that have occurred in the states are the breaking up of original heavy forests in the eastern states to create croplands, widespread drainage of wetlands almost everywhere, loss of western grasslands to cultivation and to brush through fire control and overgrazing, and general urbanization of large areas. Highways alone now take up a large fraction of our landscape. Not all habitat changes have been of negative impact to all species. The conversion of grasslands to brush has benefitted accipiters and Harris's hawks, while it has been unfavorable for grassland species such as burrowing owls. The draining of fresh-water marshes in Florida represents lost habitat for everglade kites, but in some cases it has increased habitat for caracaras. In general, however, there has been a progressive loss of suitable habitat for most raptor species in the states. No species can survive in the wild without adequate acreages of habitat to which it is adapted, and thus safeguarding habitat is the primary necessity in preventing the loss of species and in maintaining the numbers of raptors at desirable levels.

Forest Habitats

As Hamerstrom (1974) has pointed out, few raptors are birds of unbroken forests. While a number of species commonly nest in dense forest, many of these forage in edge or open habitats. The species that come closest to a dependence on extensive forests are the goshawk, the broad-winged hawk, and several of the owls, particularly barred owls, spotted owls, saw-whet owls, and boreal owls. Most other species prefer mixed habitats or open country. Such generalizations are not perfect, however. For example, the red-tailed hawk in some regions is a bird of dense forest (see Luttich *et. al.* 1970), while in other areas it is common in mixed and open country. The falcons are generally open-country birds, although merlins occupy forest in some regions. Both of the smaller accipiters, sharp-shinned hawk and Cooper's hawk, seem to be most abundant in mixed habitat, although one can sometimes find pairs nesting in heavy forest or even in quite open country. Two of the four species of kites are species of open country, while preferences of the Mississippi kite and swallow-tailed kite seem to run more toward mixed and forested habitats. The three vulture species are all essentially birds of open and mixed habitats, as are most of the buteos. Thus it is likely that in itself, the breaking up of extensive forests that occurred with settlement of this country was more beneficial than harmful to most raptor species.

The species that are most dependent on extensive forests, however, have been threatened not only by loss of much forest habitat that has occurred in some regions but also by recent trends toward shorter rotation periods in timber management. Both goshawks and spotted owls, for example, appear to be tied largely to old-growth timber for nesting. In England it appears quite clear that the Goshawk is sorely pressed by a lack of sufficient acreage of mature forest (Newton 1972). Goshawks in the U.S. are presently coming back in the eastern states in second growth timber, although in most cases it is in the most mature stands available. With shorter rotation periods it is as yet unclear that these species can adapt and survive in areas managed for timber, unless tracts are set aside specifically for their management (see discussion in Zarn 1974).

As reviewed by Snow (1973b) a number of authors have pointed out the tendency of bald eagles to utilize mature trees for nesting, and in many regions measures have been taken to safeguard eagle nest trees with buffer zones from cutting. Although this certainly appears to be a prudent policy, it has not been conclusively demonstrated that eagles will not generally move to trees of lesser stature if the taller trees are eliminated. The nesting of bald eagles on the ground in the Aleutians and in low mangroves in Florida suggests the species has some flexibility in this regard. However, it may be that even if eagles will accept relatively low nest sites when none other are available, they would succeed better if higher nest sites were available.

Certain raptors are dependent on cavities in trees for nesting, and forestry practices which remove such trees can be expected to have negative impacts on these species. In particular, kestrels and nearly all of the smaller owls are dependent on such cavities. In many cases these species can occupy holes drilled by woodpeckers, but as Tanner (1942) has shown, the abundance of woodpeckers is strongly correlated with the abundance of dead wood, and abundant dead wood is not a desirable characteristic of forests managed for maximal timber production. Some of the larger owls, such as barred owls, are generally dependent on natural cavities for nest sites, and here again it takes mature trees to supply such cavities. Although it has not been demonstrated that availability of nest sites is an important limiting factor for most hole-nesting raptors, this has been shown in many other hole-nesting birds (von Haartmen 1971). Hamerstrom *et al.* (1973) have shown this to be the case with kestrels in one region of Wisconsin. These authors were able to obtain an enormous increase in nesting populations of this species by supplying suitable nest boxes. In any event, the availability of cavity nest sites is not optimized by short timber rotation

periods or removal of dead trees. To some extent, at least, this difficulty can be corrected by provision of artificial nesting sites.

Probably one of the more significant timber management practices for raptors has been the control of fires. For example, in southern Arizona where fire control has been practiced for many decades, the character of the forest landscape has changed greatly. The open park-like stands of pine have become cluttered with oak-juniper brush, and the fire hazard now is sufficiently great that continued fire control is unavoidable. In contrast, the forests just south of the border in Mexico have largely retained their open nature (Marshall 1957). Since the forests both above the border and below have been heavily grazed it appears that fire control may have been the major factor in the vegetation changes, although the matter is in some dispute as grazing is thought to have been less severe in Mexico. Regardless of whether or not fire control was the only important factor, large areas of brush now exist where formerly there was grass. While the brush in many areas makes good habitat for accipiters, these areas are no longer habitat for kestrels. Other species have presumably been affected as well.

Open-country Habitats

Olendorff (1973) and Olendorff and Stoddart (1974) have pointed out that cultivated land is generally poor habitat for raptors. In part this effect presumably stems from chemical pollution, in part it may stem from poor food supplies or difficulties in hunting certain kinds of crop-lands, in part it may stem from human disturbance, and in part from a lack of trees for nesting in some regions. These authors present a table for nesting habitats chosen by great horned owls, prairie falcons, golden eagles, ferruginous hawks, and Swainson's hawks (table 1). This table suggests that of the species considered only Swainson's hawk is able to nest to any extent in cultivated land. However, it is difficult to judge from the table whether or not Swainson's hawks were actively avoiding or preferring cultivated land for nesting, as the relative amounts of the various habitat types available for nesting were not detailed and the relative availability of nesting trees in the various habitat types was not detailed.

Certain raptor species, at least in certain regions, appear to be fairly well adapted to cultivated lands. For example, Butts (in Zarn 1974b) reports that burrowing owls did better in prairie dog towns adjacent to wheatfields than in towns in unbroken grassland. Kestrels are a familiar species in many cultivated areas, as are white-tailed kites in regions of California devoted to forage crops.

Table 1.--Differential utilization of shortgrass prairie habitats by nesting birds of prey - northeastern Colorado, 1970-1972. Sample sizes in parentheses. Table adapted from Olendorff and Stoddart (1974).

Species	Unbroken Grasslands	Creek Bottoms	Cliffs	Cultivated Land
Swainson's Hawk				
Percent Use	30.0 (45)	63.3 (95)	--	6.7 (10)
Fledglings per Nest	1.19 (37)	0.90 (83)	--	1.10 (10)
Ferruginous Hawk				
Percent Use	57.8 (41)	35.2 (25)	5.6 (4)	1.4 (1)
Fledglings per Nest	1.73 (33)	1.33 (21)	3.00 (2)	4.00 (1)
Golden Eagle				
Percent Use	14.5 (8)	32.7 (18)	52.8 (29)	--
Fledglings per Nest	0.88 (8)	0.40 (15)	1.18 (22)	--
Prairie Falcon				
Percent Use	--	--	100.0 (30)	--
Fledglings per Nest	--	--	3.41 (27)	--
Great Horned Owl				
Percent Use	7.3 (3)	80.5 (33)	9.8 (4)	2.4 (1)*
Fledglings per Nest	1.33 (3)	1.45 (29)	2.00 (2)	2.00 (1)*

* Nest at a school house in a small town, not actually in cultivated land.

In grazed areas the impact of livestock may in some cases be beneficial and in other cases detrimental to raptor populations. Under some circumstances, heavy grazing can make grasslands more suitable for certain small mammals (see Stoddart and Smith 1943). Not only are populations of prey mammals high in these cases, but vulnerability to predation is also presumably high because of reduced cover. In the case of the burrowing owl, short stature of vegetation is beneficial and holes created by burrowing mammals such as prairie dogs and badgers are almost a necessary resource in the western states. While burrowing owls frequently dig their own burrows in the sandy soils of Florida (Courser, pers. comm.), in the harder soils of the western states burrow starts provided by mammals appear to be nearly obligatory (see discussion in Olendorff 1973). Where overgrazing leads to short stature of vegetation and increased small mammal populations, burrowing owls can be expected to thrive.

However, Olendorff and Stoddart (1973) indicate that in their shortgrass prairie study area small mammals were generally most abundant in ungrazed or lightly grazed habitat. Thus it appears to be difficult to generalize about the effects of grazing. Phillips and Monson (in Phillips *et al.* 1964) have attributed the loss of the aplomado falcon as a breeding bird in Arizona to overgrazing. This species was restricted to yucca-grassland regions which were heavily overgrazed in the 1870's and 1880's and which have never completely recovered. The

aplomado apparently nested commonly in the vicinity of the Huachuclas through the 1880's and disappeared abruptly soon thereafter. As is generally recognized in range management, excessive grazing eventually leads to plant replacements, erosion, and general deterioration of rangelands. Olendorff and Stoddart (1974) point out that considerable destruction of potential nest trees by cattle may be a very significant stress on grassland raptors. These changes can hardly be of overall benefit to birds of prey in this habitat.

For certain grassland raptors Olendorff and Stoddart (1974) argue that a lack of trees (or other elevated structures) may often be the most important limiting factor. Their data indicate that 40% of Swainson's hawk nests and 41% of ferruginous hawk nests in northeastern Colorado were in trees planted by man or on other man-created structures. These authors suggested that there may well be more Swainson's hawks in this region now than there were when the region was first settled. Nevertheless, it has not yet been demonstrated experimentally that populations of species, such as Swainson's hawks and ferruginous hawks, can be increased by increasing the availability of trees or artificial sites in grassland habitat.

For species of open country that nest on cliffs, the availability of nest sites may also be an important limiting factor in some areas. Strong evidence for this assertion has been obtained for prairie falcons by Fyfe (in Cade 1974) who has increased nesting densities in

this species by dynamiting out artificial pot-holes in otherwise nest-site-free cliffs. However, increased nesting populations were only produced in regions where mammals were the main food for the falcons. In regions where they fed primarily on birds no increases were obtained, possibly because nest sites were not a primary limiting factor there. The fact that Enderson (1964) found such inconsistent occupancy of prairie falcon territories in Colorado suggests that nest sites may not have been the primary limiting factor in his study area as well. As noted earlier, Hamerstrom *et al.* (1973) have obtained strong increases in kestrel populations in Wisconsin by increasing the supply of nesting sites. It appears that each species and each area needs to be studied individually to determine critical limiting factors. Nest sites may be important in some regions but not in others. Vast areas in the western states are abundantly endowed with cliffs, yet have low populations of cliff-nesting raptors.

Water

The importance of water supplies to raptors is obvious in certain cases and more subtle in others. Certain species, such as bald eagles, ospreys, peregrines, everglade kites, red-shouldered hawks, and black hawks, are directly and strongly dependent on aquatic habitats for food and nesting. For many of these species the very existence of marshes, rivers, lakes, and seashores in unpolluted condition is critical for survival.

The endangered everglade kite is a good example of a species obviously dependent on properly maintained aquatic habitat for survival. The nearly exclusive food of this species in Florida is the aquatic apple snail, *Pomacea paludosa*, and the kites can only exist in areas where snail populations are strong and accessible. Widespread permanent drainage of marshlands in Florida has led to a greatly restricted range for both the snails and the kites. Also, the snail appears to be slow to recover after temporary drying-out of wetlands. However, the ecology of the snail has never been thoroughly studied, and its habitat requirements are known only in a general way (Snyder and Snyder 1969, 1971).

Even where the snail is common it is not always accessible to kites. Where surface vegetation is too dense, as for example, because of dense mats of introduced water hyacinth, the kites are unable to locate food - they cannot see it. In contrast, the limpkin, another Florida bird dependent on the apple snail, can find food by touch under such conditions and can feed in such habitats (see Snyder and Snyder 1969). Thus it appears that management of aquatic habitats for everglade kites must entail

practices which maintain water levels and control the spread of surface aquatic vegetation, principally the water hyacinth. Control is complicated because of a progressive enrichment of freshwater marshes of Florida from agricultural and other practices. Although the snails appear to be able to tolerate excessively ripe water conditions, the same conditions predispose the marshes to clogging masses of surface aquatic growth. Thus the quality of water entering the marshlands is as important as its quantity, and both are currently being stressed to near capacity. Continued growth of the human population in southern Florida can only exacerbate the difficulties.

Declining water supplies have acutely stressed certain raptors of the southwestern states that are closely tied to riparian habitat, particularly black hawks and gray hawks, both of which are almost never found nesting away from such habitat (see Phillips *et al.* 1964). The lowering of water tables in southeastern Arizona has led to progressive restrictions of the ranges of these species. Glinski (pers. commun.) has recently estimated the total population of gray hawks in Arizona to be between 35 and 50 pairs. This species was formerly found all along a number of rivers as far north as Tucson (see Bent 1937), but now, with few exceptions, it is found only along the few stretches where surface water still flows. The nature of the relationship of the gray hawk to surface waters is not entirely clear, as the diet of this species is primarily lizards. The relationship of the black hawk to flowing waters is apparently much more straightforward, as its diet leans heavily toward aquatic vertebrates and invertebrates (see Brown and Amadon 1968). Both species nest characteristically in tall cottonwoods and thus are further threatened by potential removal of these trees in phreatophyte control programs (see Horton 1972, Culler *et al.* 1970).

Other species show more subtle relationships with water. In our own studies of accipiters in Arizona and New Mexico we have rarely found a pair of Cooper's hawks nesting more than a quarter mile from water, whether this be a cattle tank, pool, stream, or seep. In a great many cases accipiter nests are placed in close proximity to such sources of water. Although it is clear the relationship is not absolute, because a few pairs do nest distant from water, it appears the presence of surface water is important to these species. Whether the relationship operates through bathing and drinking, or through higher prey populations or healthier nest trees near water, is unknown. However, it is interesting to note that the incidence of predation on accipiter nests by raccoons has been very low in our study area. The general rarity of surface waters in the region may have beneficial aspects in reducing populations of this predator, a major mortality factor for raptor nests in other

regions (see Meng 1951, Craighead and Craighead 1956).

Nelson (1969) has attributed the widespread and long-term decline of the peregrine in the western states to long-term drought conditions, operating very likely through declines in water-fowl prey, but perhaps also through direct susceptibility of the peregrine to temperature stress. Porter and White (1973) have questioned the importance of these climatic changes to the peregrine decline in Utah, although they did not challenge Nelson's hypothesis for states farther north. How much of the current trend toward loss of surface waters in the western states can be attributed to man and how much should be attributed to climatic changes is not completely clear. In Arizona the losses of aquatic habitat have been enormous in the past 100 years (see Phillips et al. 1964). In part this has been due to drainage, in part to pumping of ground water supplies, in part to overgrazing, and in part to long-term climatic shifts. To what extent the climatic shifts may have resulted from man-caused changes in vegetation is problematical. Whatever the major causes, the progressive losses of surface waters in the southwestern states, if continued into the future, can be expected to prejudice the survival of certain raptor species and to reduce the populations of others. All species will not be equally affected, and some, primarily those adapted to desert conditions, may be little affected.

Elsewhere in the states, the water management practices with most significance to raptors, outside of general pollution difficulties, may be the building of dams and reservoirs and stream channelization. Impoundments such as Rodman Reservoir on the Oklawaha in Florida, have created local habitats suitable for raptor species dependent on lakes (ospreys and bald eagles), but at the same time have destroyed large areas of river bottom habitat suitable for other raptors (red-shouldered hawks, Cooper's hawks, barred owls). Whether, in the balance, the impoundments represent a benefit for raptors is debatable. All dams and reservoirs have finite lifetimes, and in a broad sense represent only short-term benefits to species such as ospreys and eagles. Stream channelization affects the movements of water and nutrients through river bottom communities, and generally involves destruction of considerable riparian vegetation. In general, such changes are presumably harmful to raptors.

Toxic Chemicals

The massive introduction of toxic chemicals into the environment that began roughly about the close of World War II has had a tragic effect on populations of certain raptor species. In fact, it is largely through the effects of these chemicals on birds of prey that the menace of

environmental poisons has achieved public notice. The compound of most far-reaching significance to raptors in North America appears to have been DDT (especially its metabolite, DDE), although other compounds, particularly dieldrin, and various mercurials, have had important impacts in more local contexts. The effects of these poisons on raptors have been extensively studied, and the broad picture of stress that has emerged is quite compelling.

The species that have been most severely stressed are ones that occupy positions that are high in natural food chains. This effect appears to be a direct result of the fact that the concentrations of many stable toxicants tend to increase as one proceeds up food chains, and the fact that the primary route of exposure of raptors to these toxicants is through their diets (see Woodwell 1967, Robinson et al. 1967). In general, the more steps in a food chain, the greater the contamination at the end of the chain. Thus the raptors specializing on birds or large fish in their diets are the species that have suffered the most, as these prey are themselves generally high in food chains. Examples of bird and fish-eating species that have suffered at least regional declines thought to have been caused by biocides are the peregrine, the prairie falcon, Cooper's hawk, sharp-shinned hawk, merlin, osprey, and bald eagle (Cade et al. 1971, Fyfe et al. 1969, Snyder et al. 1973, Fox 1971, Hickey and Anderson 1968, Krantz et al. 1970, Wiemeyer et al. 1972). In contrast, most raptors concentrating on mammals or insects in their diets have maintained relatively stable populations (see Hickey and Anderson 1968). Most mammals that are prey of raptors are herbivorous, only one step removed from the bottom of food chains, and the same is true of many insects. Direct measurements of contamination of such prey have shown them to be relatively clean (e.g. Lincer and Sherburne 1974). Thus the kites, the buteos, and the owls have fared quite well as far as pesticide stress is concerned.

The relative vulnerability of various species to poisons such as DDE can be seen almost diagrammatically with the three North American accipiters (Snyder et al. 1973). Both Cooper's hawks (Accipiter cooperii) and especially sharp-shinned hawks (Accipiter striatus) prey heavily on small birds, and both species have suffered severe declines in the eastern states since 1947, the generally accepted year for first widespread use of DDT. In contrast, goshawks (Accipiter gentilis) feed heavily on mammals, and the birds they take are often large herbivorous species, such as grouse and pigeons (see Storer 1966). Goshawks have been spared the declines suffered by the other two accipiters, and in fact, appear to be increasing in recent years in the eastern states. Direct measurements of DDE in eggs of the three accipiters confirm exactly what one

might predict from the trophic positions of the species. Sharpshins tend to be heavily contaminated, Cooper's hawks less so, and goshawks even less.

The primary detrimental effect of DDE on raptors has been one of eggshell-thinning rather than direct lethality. A correlation of the extent of eggshell-thinning with concentrations of this compound in eggs has been demonstrated in a great variety of species (e.g. Cade et al. 1971, Hickey and Anderson 1968, Enderson and Berger 1970, Fyfe et al. 1969). With sufficient thinning eggs become sufficiently fragile that they are easily broken. Poor hatchability of eggs appears to be the primary difficulty that has developed with most affected species. However, the dose-response relationship appears to vary somewhat with the species (see Blus et al. 1972). Certain species, such as the herring gull, exhibit little eggshell-thinning even with relatively high concentrations of DDE, while other species, such as prairie falcons and Cooper's hawks, appear to be very sensitive to DDE. In general, the response curve follows a logarithmic pattern. Thus as the concentration of DDE increases in eggs the rate of decrease of eggshell thickness declines. Population declines have generally been associated with declines in thickness on the order of 20% or more.

Although attention has been focused on the eggshell-thinning effect, there is some evidence that DDE may also have other detrimental effects, for example, increased embryonic death (see Heath et al. 1969, and Koeman et al. 1972), and behavioral abnormalities (Peakall 1970). In our own studies of DDE levels in accipiters three pairs of Cooper's hawks that exhibited disturbed behavior also had relatively high concentrations of DDE in their eggs, while they were not heavily contaminated with heavy metals or other pollutants. In two of the three cases nest-building was abnormal, in the third case prey transfers from male to female were disturbed. While three is a minute sample size, these results are suggestive. Hamerstrom (1970) also has attributed recent changes in prey transfer behavior in harriers to contamination with pesticides, although supporting data were not provided. In addition, we noted that while egg-breakage was frequent in Cooper's hawks and DDE was high in broken eggs, not all broken eggs were exceptionally thin, and several appeared to have been punctured by the talons of the female adults. Ratcliffe (1970) mentions similar apparent problems with egg care in the pesticide-stressed peregrine populations of Britain. Peakall (1970) discusses still another behavioral effect that appears to be related to DDE and other organochlorines - delayed breeding. Particularly in birds of prey, where timing of breeding appears often to be critically related to cycling of prey populations, such delays can be expected to have depressing effects on

reproduction.

Analyses of tissues of a number of raptors found dead in the U.S. and Europe have yielded concentrations of dieldrin that appear to be high enough to have been lethal (Jefferies and Presst 1966, Koeman et al. 1969, Reichel et al. 1974), and it appears that this compound, much more so than DDE, has been depressing raptor populations through direct mortality of adults. It seems likely that dieldrin, rather than DDE, was the major stress factor in declines of several raptors including the peregrine in Europe (see Ratcliffe 1970, Lockie and Ratcliffe 1964, Koeman et al. 1972a). Evidence that dieldrin causes eggshell-thinning has been spotty and not entirely convincing (Ratcliffe 1970, Enderson and Berger 1970, Peakall 1970). However, this compound has demonstrated a strong capacity to induce hormonal changes, and may be important in a number of the sub-lethal ways discussed above with DDE.

Mercury, like DDT and dieldrin, is stable and can show biological magnification up food chains (Peakall and Lovett 1972, Fimreite 1974, Borg et al. 1970). The impact of the various mercurial compounds on raptors, however, appears to be mostly local in character. A principal route of introduction of mercurials into the environment has been seed-dressings for grains, and consequently some problems in North America have developed in the great plains region. Fimreite et al. (1970) report levels of mercury in eggs of raptors in Alberta that are sufficiently high that they may be having effects on egg-hatchability. Another local impact of mercury has been with aquatic birds near a Canadian chlorine plant (Fimreite 1974). In general the effects of mercury are diverse. Important effects seen have been decreased hatchability of eggs, and kidney and nervous system damage. Little or no eggshell-thinning appears to result from contamination with the organic forms of mercury found generally in wildlife tissues (Peakall and Lincer 1972), although Stoewsand et al. 1971 found eggshell-thinning to be produced by mercuric chloride. In several cases eagles have been found dead with high enough levels of mercury to be considered directly lethal (Anonymous 1970, Koeman et al. 1972b).

Another group of compounds with potential impacts on raptors are the PCBs (see Peakall and Lincer 1970, Risebrough et al. 1968, Dustman et al. 1971). The PCBs appear to have little if any capacity to thin eggshells (Risebrough 1972, Peakall 1971, Heath et al. 1970), but they are especially potent in enzyme induction and resultant hormonal disturbances, and may have played an important role in some of the sub-lethal ways discussed above for DDE. Hays and Risebrough (1972) have called attention to a possible teratogenic effect of dioxin contaminant of PCBs with terns, but to our knowledge the effect has not yet been clearly demonstrated to be from this cause. PCBs have been shown

to increase embryonic mortality (Tumasonis *et al.* 1973) and to cause feather loss (Vos and Koeman 1970), and their high concentrations in raptor tissues in certain areas give cause for general concern.

The stability of many of the important toxicants has led to potentials for transport of these materials to regions distant from their points of release into the environment. Significant movements of DDT occur through the atmosphere, and the primary input in many areas is in rainfall (see Woodwell *et al.* 1971). Birds of prey face complicated patterns of exposure when they themselves are migratory or their prey are migratory. Lincer and Sherburne (1974), for example, found that concentrations of DDE in local prey populations of breeding American kestrels in the Northeast were insufficient to account for levels of DDE found in the eggs of the kestrels. They assembled considerable evidence to suggest that these birds were contaminated primarily on their wintering grounds in the southeastern states. Similarly, Finnish peregrines may have acquired most of their contamination on their wintering grounds in southern Europe, or again, through their diet of migratory prey on the breeding grounds (Linkola and Suominen 1969). The same may be true of peregrines breeding in the arctic in North America (Cade *et al.* 1971). The global movements of stable toxicants used in management of crops and forests mean that a full evaluation of the effects of a particular application is not easily made.

Particularly in the western states, where many raptors or their prey winter south of the Mexican border, we are in a position where we cannot fully control the management of these raptor species. Where use of a biocide in one country affects wildlife in another the problems of control may in some cases be insoluble.

The recovery of the peregrine occurring in Britain in recent years, following curtailment of use of a number of organochlorines, is one of the clearest pieces of evidence that these chemicals were instrumental in the declines (Cade 1971). With recent federal actions to restrict the uses of DDT and dieldrin in the U.S. there is hope that the peregrine and other stressed species in this country may also begin to recover. Recent studies are showing falling levels of DDT compounds in small birds of the eastern states (Johnson 1974) and there are some hopeful signs from counts at Hawk Mountain, Pennsylvania that declines of a number of species in the eastern states have levelled off, for example, Cooper's hawks and sharp-shinned hawks. Clear recovery has not yet begun, but there are grounds for optimism.

Shooting

In general, diurnal raptors make large and attractive targets to gunners, and despite legal protection in most states the shooting of raptors still continues. Most band returns for diurnal raptors are reported as shot, and presumably many, if not most banded raptors reported as found dead were in reality shot. If adjusted for reporting rates and losses due to crippling, these banding returns can give us estimates of shooting pressures on raptors (see Geis 1972). Henny and Wight (1970) have made such estimates for Cooper's hawks and red-tailed hawks (table 2).

Table 2.-- First-year shooting mortality of Cooper's hawks and red-tailed hawks computed from band returns. Table adapted from Henny and Wight (1970).

Species and Years	Recovered Shot (%)	Recovered Overall (%)	Mortality Due to Shooting (%)
Cooper's			
1929-1940	15.7	20.9	28 - 47
1941-1945	8.3	11.5	15 - 25
1946-1957	6.8	9.5	12 - 21
Red-tail			
1926-1940	7.1	9.2	13 - 20
1941-1945	7.5	9.0	14 - 20
1946-1957	7.3	10.9	13 - 24

Their estimates of first-year shooting mortality are calculated from the recovery rates using a waterfowl-derived crippling loss rate of 28.6% and waterfowl-derived reporting rates of 63% to 78.5%. These reporting rate figures are relative-high for waterfowl, as most rates calculated for the 1950's have been around 50% (see Geis and Atwood 1961). Consequently, if reporting rates for raptors resemble those for waterfowl the mortality rates given in table 2 may be conservative. Unfortunately, no studies have been made of reporting rates for banded raptors.

Especially with raptors one might expect reporting rates to be declining in recent decades as raptors have been given increasing legal protection. Not all gunners know that the banding office does not prosecute. Thus although the data of Henny and Wight suggest declining shooting rates of Cooper's hawks from 1929 to 1957, and stable shooting rates for red-tailed hawks during the same period, there is no easy way to confirm the validity of these trends. It is possible that actual shooting rates of Cooper's hawks have declined not at all, while reporting rates have declined to produce the declining

recovery rate. In Britain, where raptors have likewise been given increasing legal protection in recent decades, there has been a suspicious decline in the percentage of banded raptors reported as shot and an increase in the percentage reported as found dead (Glue 1971, Brown 1974).

In any event the shooting rates for both Cooper's hawks and red-tailed hawks appear to be substantial, sufficiently so that Henny and Wight believed shooting alone could largely account for a population decline in Cooper's hawks reported by Bent (1937) in the early part of this century. As these authors point out, the recovery rates for Cooper's hawks and red-tailed hawks are comparable to or exceed the recovery rates of many species of waterfowl, which, of course, are legally shot (and many of which have high reproductive rates).

In recent years the recovery rates for raptors have dropped to very low levels, on the order of one or two percent for many species, and the general feeling seems to be that the effect may be due more to drops in reporting rates than to drops in actual shooting rates. Reporting rates in general for game birds have been dropping in recent years and now tend to run a little over 30% (Martinson 1966, Martinson and McCann 1966, Tomlinson 1967).

Directly documenting the impact of shooting on raptor populations is often a difficult task, largely because raptor populations are open systems and shooting is not the only factor operating on them. Nevertheless, there are some reports that suggest strong impacts in at least certain cases. Ellis *et al.* (1969) have provided some statistics on the extent of mortality of raptors along a 12.1 mile road paralleling a power line in Utah for 1967-1968. In their year and a half study they found an average of 3.14 raptors per mile under utility poles, primarily golden eagles, with lesser numbers of bald eagles, buteos and other miscellaneous species. They found mortality, at least most of which was believed to be from shooting, to be highest in fall and winter, the season of heaviest sport hunting in the area. They emphasized the high vulnerability of raptors on utility poles paralleling roads and the gross disregard for the law protecting raptors that appeared to exist. However, to what extent the mortality observed may have been due to electrocutions, and to what extent the mortality was affecting raptor populations, local or otherwise, were not documented.

Shor (1970) has estimated that over half of the first-year peregrines wintering on the Texas coast end up shot. How much impact this has had on breeding populations is likewise unknown. In England peregrines were systematically shot out during World War II because of the threat they posed to carrier pigeons (Ratcliffe 1969). The shooting was effective

and the peregrine was essentially wiped out in southern England. However, by 1955 recovery was almost complete in some regions.

Wanton shooting and scientific collecting were likely an overwhelming stress on various populations of the California condor, especially around the turn of the century (Wilbur ms). Wilbur has found evidence of 177 condors and 71 condor eggs taken for scientific collections. At least 111 birds and 49 eggs were taken between 1881 and 1910 alone. In addition, wanton shooting accounted for at least 40 more birds between 1806 and 1960 (probably a strong underestimate of actual numbers shot). Apparently the disappearance of the condor from various parts of the historic range coincided with peaks of collecting activity in those same areas. Since 1960, however, there have apparently been no confirmed losses from shooting, and the major problem for the condor in recent years clearly has been poor reproduction.

The endangered everglade kite still suffers significantly from shooting losses despite increasing publicity as to the plight of this species. Sykes (pers. commun.) reports that it is still frequent to see kites with gunshot holes in their wings following each hunting season, and two were known killed by shooting in 1970.

Shooting may be a factor in the decline of the caracara in Florida to a total population estimated at about 100 birds in 1970 (Heinzmann 1970). This relatively tame species is quite vulnerable to the gun because it commonly forages along roads for carrion and perches on roadside poles and fences. Reputedly, some persecution of this species has resulted from the belief that it kills newborn cattle, but the major problem may be indiscriminate gunners looking for targets.

Sprunt (1972) and Retfalvi (1965) have considered shooting to be one of the major problems faced by the bald eagle. The bounty on bald eagles in Alaska is estimated to have resulted in over 100,000 eagles shot from 1917 to 1952 (or approximately 3,000 per year) a rate of predation with unknown impact on the population. Current estimates of the Alaskan population indicate 35,000 to 40,000 birds and at least reasonable stability (Snow 1973b). With the golden eagle Spofford (1964) estimated that over 20,000 birds had been shot in the Texas - New Mexico region during the 1940's and 1950's. These were almost entirely wintering birds. The impact of this shooting on breeding populations from which they were derived is unknown. Current estimates as to the total number of golden eagles in North America range up to 100,000 birds (Huegley, in Snow 1973a).

Newton (1972) presents a valuable analysis of the effects of shooting on golden eagle populations in Britain:

"Despite findings on the effects of eagles on sheep and grouse eagles are still widely shot. However, since this is illegal, it is exceedingly difficult to study. At its most intense it may permanently prevent eagles from settling in an area. Birds may move in every year but be killed so quickly that the outsider knows nothing of it; he only sees suitable habitat unoccupied. Within the regular range of the Golden Eagle, Sandeman (1957) compared the success of birds nesting on deer ground with that of birds nesting in sheep and grouse areas [Table 3]. On deer ground there was no instance of an eagle lacking a mate, but on sheep and grouse ground eight such instances were recorded. On deer ground there was no instance of an eagle paired to an immature partner, but on sheep and grouse ground there were four such instances. Both these factors are symptoms of excessive shooting. An immature partner in a pair meant that the birds either did not lay or produced infertile eggs. The mean size of successful broods was the same in both areas, but the overall brood size, when pairs that raised no young are taken into account, was 0.6 on deer ground and only 0.3 on sheep and grouse areas. In the latter areas killing of eagles was suppressing breeding success so much that this population could not have been sustained without continual immigration.

"Thus the success of the Golden Eagle in Britain is determined by the prevailing land use and the human attitudes fostered thereby. There is no ecological reason why the species should not breed over more of Britain than it does. Young are produced every year, but apparently most are absorbed by killing within the regular range or in the areas they try to colonise. The situation has improved slightly in the last 20 years in that the species is now being allowed to remain in a few areas from which it was formerly eliminated. On the other hand persecution is increasing in the Highlands, especially on grouse moors. Hence, the future of the bird probably depends mainly on future trends in land use, particularly on the extent of game preservation. If more eagles are killed, their numbers

can be expected to decline and their range contract."

In general, the impact of shooting appears to increase with the size of the raptor (Brown 1974), probably because of the conspicuousness of large raptors. Diurnal raptors seem to suffer much more than nocturnal ones (Glue 1971). While we have found no clear examples where the impact of shooting has been sufficient to wipe out any raptor species more than locally, very likely the populations and densities of many species have been and continue to be strongly affected. One need only visit a country such as Guyana in South America which has rigidly enforced laws prohibiting firearms, to realize how abundant and relatively tame raptors can become in the absence of shooting. Similarly, White (1969) has remarked on the conspicuous abundance of raptors in one region of Utah protected from shooting pressures.

Miscellaneous Impacts of Man

Raptors vary enormously in their tolerance of human disturbance around nests, and even within species it is difficult to generalize about vulnerabilities to disturbance. In general, it appears that most individuals of most species have strong drives to persevere in nesting-attempts even in the face of considerable human harassment. Desertions of nests are most likely to occur in the early stages of nesting. Olendorff and Stoddart (1974) claim that the ferruginous hawk is one of the most susceptible species to human disturbance, and they recommend that nests of this species not be climbed before young are present. Likewise golden eagles appear to be generally intolerant of disturbance around the nest. With ferruginous and Swainson's hawks Olendorff and Stoddart (1974) have compared nesting success in areas free from human human disturbance to nesting success in areas where there was free access for man: for 39 nests of ferruginous hawks in remote or posted areas they found a fledging success of 1.95 young per active nest, while in 18 nests in areas of free access they found only 1.06 young per nest. Comparable figures for Swainson's hawks were 1.24 and 1.00 young per nest for 49 and 55 nests, respectively. In neither case were differences statistically significant at the 5% level, although the comparison for ferruginous hawks was significant at the 10% level.

Effects of human disturbance on nesting raptors have been studied in several other cases. Grier (1969) investigated the influence of climbing Ontario bald eagle nests on later productivity of these nests and found no effect. Mathisen (1968) checked productivity of bald eagles in Minnesota as a function of isolation from man, and he likewise found no significant effects. However, the degree of disturbance in both of these studies may have been generally below levels where effects might have been seen.

Table 3.--Effects of persecution on golden eagles, South Grampians 1950-56. Table adapted from table 7 of Newton (1972).

	Deer Ground	Sheep/ Grouse Ground
Number of Records	24	51
Only One of Pair Present	0	8
One Partner Immature	0	4
Young per Successful Nest	1.4	1.4
Young per Pair with Eggs	0.6	0.3
Original Data from Sandeman (1957)		

In our own studies of accipiters in the southwestern states we have been impressed by the general boldness of Cooper's hawks, a species described as often very wary by Bent (1937), Meng (1951), and Craighead and Craighead (1939) in the eastern states. It may be that where these birds are heavily persecuted by man they become much more sensitive to human activities near nests, that is, the effects of human activities on nesting may vary as a general function of levels of persecution by man on a regional basis. The effects of human disturbance on nesting of accipiters has been the subject of a recent study by Steve Hennessey in Utah, but results have not yet been published.

Unfortunately, in many regions the sorts of habitats favored for nesting by raptors are also the same habitats that are favored by man for recreational and other activities. In Arizona it is the canyon bottoms and riparian zones that are disturbed primarily by hikers and picnickers. Yet nesting of a number of species of raptors, for example, gray hawks, zone-tailed hawks, black hawks, and Cooper's hawks, is concentrated heavily in the same areas. In other areas disturbance of cliff-nesting raptors by rock-climbers has been a locally important problem (see Herren 1969, Snow 1972, Enderson and Craig 1974). In still other areas boating activities are steadily increasing the levels of disturbance at osprey and eagle nests. On occasion nests of these species have been unmercifully harassed by photographers.

Another important human impact on raptors that has gained some attention in recent years is electrocution, especially of eagles, on utility poles and electrified fences (see Olendorff 1972, Boeker 1972, Boeker 1974, Stewart 1973). Although we have seen no estimates of total impact of electrocution on eagles, the local impact has been considerable in certain regions. In places investigators have found more electrocuted eagles than utility poles. Boeker (1972) reported approximately 300 known electrocutions of eagles since 1970 in an area he considered to be only a minute sampling of the entire range of the eagles. With recognition of the problem of electrocution, however, steps have been taken to render utility poles innocuous in various regions of particularly heavy use by eagles (Boeker 1974).

Even when not electrified, wires strung from poles or fences present some risks, and it appears that collisions of raptors with wires are a regular source of mortality (see Weir 1971, Glue 1971). Herren (1969) suggested that wires of various sorts may have been the primary factor in extirpation of the eagle owl from the greater part of its range in Switzerland. The closely-related great horned owl in this country has likewise been killed with some frequency by collisions with

wires (see McCarthy 1973, Edeburn 1973).

Collisions with automobiles and trains are another significant source of raptor mortality, though again one that has been little studied. White (1969) remarked that migrating rough-legged hawks are subjected to frequent road death in Utah, mainly as a result of their feeding on road-killed jack rabbits. For one 160-mile stretch of highway in one week of 1961 he reported 19 freshly-killed roughlegs and 8 dead horned owls. This total was presumed to have been a strong underestimate of actual mortality. From an analysis of band recoveries Glue (1971) concluded that there had been a strong increase in mortality of raptors in Britain from collisions with vehicles, an increase he attributed to increased speed and density of traffic. He found that collisions with vehicles appeared to be a much greater problem for nocturnal raptors than for diurnal ones, while the reverse was true for collisions with stationary objects such as wires and windows.

While the sorts of stress discussed above do not appear to be overwhelming when considered singly, the total impact of these stresses appears to be generally increasing. When coupled with other stresses such as shooting and falconry, it seems likely that human pressures on raptors probably provide sufficient impact that raptor populations remain significantly depressed from what would otherwise be the case in many regions.

SOME POSITIVE STEPS TO MANAGE RAPTORS

As yet comprehensive management efforts on behalf of birds of prey have been limited for the most part to rare and endangered species such as bald eagles, ospreys, condors, and everglade kites. However, recommendations for management of other raptors have been increasing rapidly in recent years. Some principal contributions along these lines have been made by Olendorff (1973), Olendorff and Stoddart (1973, 1974), Snow (1972, 1973a, 1973b, 1974a, 1974b, 1974c), and Zarn (1974a, 1974b). While an emphasis on methods to save rare and endangered species seems appropriate, in the long run one may hope for a broader program to develop so that species currently in reasonably good shape do not end up in the endangered category.

Management techniques may range from efforts to eliminate electrocution of eagles by modifying utility poles to efforts to establish captive breeding populations of peregrines, but by in large the most significant efforts will probably continue to be along the lines of safeguarding habitat and improving habitat that has been degraded. It appears now that the peak of chemical stress on raptor populations in this country and Canada has past, hopefully in time to save such species as the peregrine, but efforts to reduce chemical contamination of the

environment as far as possible remain a critical need for the near term, at least. Reduction of shooting stress, reduction of general human harassment and disturbance, and control of the impact of falconry on wild populations promise to be some of the more difficult problems in a political sense, while it is unclear that a great deal can be done to reduce mortality resulting from collisions with vehicles and wires.

Habitat Preservation and Improvement

In general, the most important limiting factors for many raptor species are probably food supplies and nesting sites. For example, insufficient, erratic, or poorly-located food supplies are a critical problem faced by everglade kites and condors. In the case of the kite it appears likely that the species can be saved if its food supply of aquatic snails can be guaranteed through habitat improvement and management. Although it is impractical on social and economic grounds to adopt a goal of returning the everglades to their former extent and quality, it does seem within reason to seek to intensively manage enough habitat to preserve the species in a few portions of its former range. A kite-management area has been set up in the Loxahatchee National Wildlife Refuge near Delray, Florida, and some success has been achieved in attracting kites into this area for nesting. The kites are mobile birds, well adapted to move when conditions become unfavorable, so it is reasonable to hope they will adopt good managed habitat on their own if enough such habitat can be provided in time. The kite population has fluctuated around 100 individuals or so for a number of years now, but recent droughts and increased demands for water from the glades have led to progressive habitat deterioration. The federal government is tentatively planning to begin land acquisition for kite management areas in 1977. Presumably the major problems beyond land control will be control of water supplies and control of aquatic weeds.

In the case of the condor, Wilbur (1972), and Wilbur *et al.* (1974) have argued that the location of adequate food supplies relative to nest sites may be presently the most severe problem. In recent years very few pairs have attempted breeding in the traditional nesting areas in the Sespe region, and it appears that local food supplies have become much poorer there than they were formerly. Instead of breeding, many condors have been congregating in regions that lack nesting sites. The drop in food supplies in the Sespe region traces to progressive loss of habitat to land development and to changed ranching practices which now leave few carcasses available for the condors.

A program of providing carcasses, primarily of deer, was begun in the Sespe region in 1971. Results so far have been promising, but not overwhelming. Condors have fed upon the carcasses with regularity, and reproduction from 1971-1973 in this area was stronger than in the previous three years: three young versus one young fledged for the two periods, respectively.

Nelson (1969) provided some evidence that declining food supplies may be the primary reason for a long-term decline of the peregrine falcon in the western states. Thus even with curtailment of chemical stress on this species its capacities for recovery in the western states may be limited. As Enderson (1969c) has pointed out, peregrines in the western states are very spotty in distribution, occurring primarily in areas of waterfowl concentrations. Success in restoring the peregrine in the west may depend importantly on successful waterfowl management.

For many other species it is also likely that food supplies are of major importance in determining distributions and abundances. Olendorff (1973b) argues that the absence of golden eagles and ferruginous hawks on the grounds of the Hanford Reservation in Washington is likely traceable to a rarity of rabbits in the region, although the habitat appears suitable for occupancy in other respects.

In other cases the primary limiting factor appears to be nest sites, as demonstrated for kestrels by Hamerstrom *et al.* (1973) and by Fyfe (in Cade 1974) for prairie falcons in Canada. Olendorff and Stoddart (1974) have recommended planting of trees in grassland areas to establish nesting populations of Swainson's hawks and ferruginous hawks. The increase in one nesting population of ospreys in Michigan apparently produced by provision of artificial nesting platforms by Postupalsky and Stackpole (1974) gives good evidence that this species is sometimes limited by nest sites. However, success was achieved only on one of the two reservoirs given the artificial sites. Failure on the other reservoir was attributed to declining fish populations. Artificial nest sites for ospreys have also been tried in California with some apparent success (Garber *et al.* 1974).

Another species for which artificial nest sites have proved to be of some value is the everglade kite (Sykes and Chandler 1974). The problem here, as with the ospreys studied by Postupalsky and Stackpole, has been not so much that the birds have nowhere to nest, but that they commonly attempt to nest in substandard sites. In the case of the kites, nests have commonly been placed in emergent aquatic vegetation too weak or growing too fast to support the nests adequately. In recent years several of these precarious nests have been transferred to nearby artificial basket structures with apparent gains in nestling production.

Preservation of sufficient habitat in undegraded condition is the critical necessity for a number of species of raptors with specific habitat requirements in the southwestern states. Of special concern in Arizona are Harris's hawk, a species primarily limited to flatland saguaro habitat; aplomado falcon, a species formerly nesting and still occasionally seen in yucca-grassland; and black, gray and zone-tailed hawks, species that are found nesting in wooded canyon-bottoms of the southern part of the state, particularly those with surface waters. In the case of Harris's hawk much of the remaining saguaro habitat is being rapidly destroyed by homesite development (Mader, pers. commun.). Apparently the species is not common on the lands included in Saguaro National Monument, possibly because the monument includes little flatland acreage. Unless substantial amounts of flatland saguaro habitat can be secured it appears that the future of the species in this region is in question. It appears that if Tucson and other neighboring cities could be encouraged to stop growing or to grow vertically instead of horizontally, the species might have a reasonable chance to persist. Harris's hawks have proved to be fairly flexible in respect to human disturbance short of shooting, but the species cannot be expected to change its habitat preferences in the face of intensive real estate development. In Texas Hamerstrom (1974) reports that widespread conversion of brushland to grassland is currently threatening the other major population of Harris's hawks in the United States (a different sub-species).

Black, gray, and zone-tailed hawks characteristically nest in cottonwoods along rivers such as the Santa Cruz, San Pedro, and Verde in Arizona. Of the three species zone-tails seem to be the least restricted to such habitat. Unfortunately, nearly all riparian habitat in southern Arizona has been managed for other goals than raptors. In some regions real estate developments are steadily decreasing the remaining acreage. The proposed Central Arizona Project would destroy large areas of prime habitat along the Verde, Gila, and San Pedro Rivers. These changes alone could be enough to cause the loss of these species in the southern part of the state, but they are not the only threats. In most areas the primary land-use of riparian habitat has been for cattle. One effect of grazing has been the destruction of sapling cottonwoods, and this critical nesting tree for these species is not replacing itself in many areas. For example, Glinski (pers. commun.) reports that prime gray hawk habitat along Sonoita Creek has young cottonwoods only in areas fenced from cattle. Other threats include dropping water tables and invasion of riparian zones by salt cedar, which now forms impenetrable thickets in some riparian areas.

The future of black, gray, and zone-tailed hawks in southern Arizona appears to be precarious. While zone-tails and black hawks also occur in lesser numbers in other regions in Arizona, New Mexico and Texas, southern Arizona appears to be a stronghold for these species in the United States. Gray hawks are almost completely limited to southern Arizona. The Sonoita Creek reserve and the Aravaipa Canyon reserve, as important as they are for these species, cannot be considered adequate acreage to insure their survival in the avifauna of the United States.

It is presently unclear what prospects there may be for reestablishing viable populations of aplomado falcons in Arizona. It seems likely that there can be little chance for success without comprehensive management of large areas of yucca-grassland with little or no grazing pressure from cattle.

Toxic Chemical Control

With the ban on DDT and current cancellation proceedings on aldrin, dieldrin, heptachlor, and chlordane, the most important of the toxic chemical stresses on raptorial birds in this country appear to be on the way out. Still there are pressures to relax restrictions. The 1974 emergency DDT program for tussock moths in the northwestern states (426,559 acres sprayed at approximately .75 pounds per acre) has not yet been fully evaluated, although a preliminary report we have seen (Herman 1975) suggests that the outbreak of moths would have collapsed almost as fast without spraying as it did with spraying. As far as the birds of prey are concerned, the effects of such spraying campaigns can now be predicted with relative confidence. Whether the sacrifice of raptors and other wildlife in the region affected are felt to be an acceptable price for the presumed benefits of the spraying campaign is a question outside the scope of this paper. In the long run it appears the only solution which will benefit both man and raptors will be continued development and implementation of alternative means of pest control.

Reduction of Shooting

Present disregard for laws protecting raptors from shooting suggest that more stringent laws would accomplish very little unless greatly expanded enforcement and education were implemented simultaneously. As an enforcement problem effective protection of raptors from shooting verges on the impossible. The best approaches at present may be indirect ones of educating the public to values of raptors and reducing the vulnerability of

raptors to shooting by such things as closure of critical areas to public use. Significant benefits might be achieved simply by siting of power lines out of gunshot range of highways or by shifts to underground cables, a suggestion with little apparent economic feasibility in the case of existing lines but one that might be worth some thought in siting of future lines. The publicity given to rehabilitation programs for shot raptors may be of far more significance in the long run than the actual rehabilitation process. Prohibiting the use of firearms, or even reducing it significantly, does not seem to be in the cards at present.

Minimizing Miscellaneous Impacts

As discussed earlier, Olendorff and Stoddart (1974) have presented data to suggest that nesting success of Swainson's hawks and ferruginous hawk is higher in areas not subjected to human disturbance. These authors believe that posting of lands and general policies of restricting human access to raptor nesting areas may be of significant benefit. Comprehensive programs to prevent timbering and other disturbances in zones around bald eagle nests have been initiated by the Forest Service and the Department of Interior, and the Audubon Society has also been active in the same regard. The Forest Service has recently instituted similar guidelines for peregrine eyries. Cade (1974) recommended that eyrie wardens be organized, possibly utilizing volunteer labor, to protect remaining peregrine nesting sites. Such guarding may be necessary in the case of well-known peregrine eyries, but extending such protection to nests of less endangered species is clearly impractical. Much benefit in general could be achieved if siting of trails and campgrounds in forested areas could be arranged so as to minimize human disturbance to nesting raptors. Unfortunately, raptor habitat preferences and human habitat preferences often coincide.

While all these measures are valuable it is questionable how much impact they may have in the long run in the face of rapidly increasing human pressures on remaining wild areas. The expanding use of off-trail vehicles is one of the more worrisome threats to raptors in certain areas. Unless enforcement of laws and regulations protecting critical habitats and species from human pressures can be increased it is likely that problems will continue to worsen.

Outside of support for lower speed limits there is probably little that can be done to reduce rates of vehicle collisions with raptors. While some benefit regarding collisions with wires might be achieved by policies of buried power and phone lines, it is not clear how much

difference this might make. It should be borne in mind that certain raptors, particularly kestrels, may be achieving a net benefit from the presence of overhead wires, as wires provide hunting perches in some areas devoid of alternative perches. This topic has not received any comprehensive study as yet.

Some Emergency Conservation Measures

Olendorff and Stoddart (1974) have made a number of proposals for increasing raptor populations:

1. Development of new nest sites
 - a. Elevated platforms, barrels, nestboxes etc.
 - b. Tree plantings
 - c. Blasting holes in cliffs
 - d. Management of other species that provide nest sites for raptors, e.g. burrowing mammals, crows, ravens.
2. Introduction of new raptor breeding stock from captivity
 - a. Release of adults
 - b. Placement of fertile eggs under foster parents in the wild
 - c. Placement of nestlings under foster parents in the wild
 - d. Controlled release of juveniles through "hacking"
3. Increasing production of young in the wild
 - a. Nest site improvements
 - 1). Conservation of trees - fencing from cattle, etc.
 - 2). Artificial nests to replace defective natural ones
 - 3). Limiting public access to nests
 - a). Posting land
 - b). Blanket prohibitions of unauthorized public use of selected federal lands during critical nesting periods
 - c). Protective legislation
 - d). Eyrie wardens
 - 4). Enlargement of ledge and cavity nests of inadequate size.
 - b. Egg manipulations
 - 1). Removing first clutches for captive rearing and encouraging of laying of second clutches
 - 2). Progressive removing of eggs of indeterminate layers
 - 3). Artificial incubation of thin-shelled eggs
 - c. Nesting manipulations
 - 1). Transfers of runts to nests with sub-average brood size
 - 2). Field treatment of diseases and parasites.

Many of the above recommendations represent untested emergency techniques for saving severely threatened raptors in the wild or for reintroducing raptors into areas where they have been extirpated. However, to some extent it appears

the authors envision more general applications of the techniques.

Currently, considerable attention is focused on the attempts of Cade and his associates at Cornell to reestablish peregrines in the wild in the eastern states. The primary technique will be controlled releases of fledged young at selected eyrie sites (see Cade 1974a, 1974b). These birds will be subsidized with food until they become competent at hunting in the wild, a falconry technique known as "hacking". Although it may take releases of considerable numbers of birds before some do become established in the wild, the chances of success in the long run appear to be relatively good, now that captive breeding of the species is starting to yield significant numbers of birds. One question currently under debate is to what extent releases should be limited to races of the peregrine native to the areas of releases. The consensus appears to be that this is an important question, and that where possible efforts should be made to restrict establishment in the wild to subspecies appropriate to the regions of release.

Monitoring Wild Populations

Regardless of one's goals concerning raptors, it appears that there is a need for more comprehensive monitoring of raptor populations than there has been in the past, as without reliable information about numbers and trends it is difficult to make rational decisions. Migration counts, such as those at Hawk Mountain, Pennsylvania, have had only limited usefulness because of a lack of standardization of counting methods and weather fluctuations over the years, and because of a lack of knowledge as to what breeding populations are being counted. It appears that there is no substitute for intensive surveys during the breeding season. This can be a relatively expensive proposition. We emphasize again the importance of monitoring populations in poor habitat as well as in good habitat. Most raptor studies have understandably been conducted in good habitat for reasons of efficiency. But when one is attempting to determine the importance of various human impacts on raptor populations, one can expect to see effects first and most dramatically in marginal populations. With increased public interest in the birds of prey, increased attention to the health of the resource is in order.

SUMMARY

To date few raptor studies have been addressed specifically to the subject of raptor management or conservation. Raptor management is a new concept with as yet poorly defined

and to some extent contradictory goals. While much information of importance to raptor conservation has been gained through studies aimed at other goals, progress toward comprehensive understanding of what is needed to sustain healthy raptor populations is still in its initial stages. Documentation of the effects on raptor populations of various factors such as grazing, shooting, and falconry, is still far from exhaustive, and present management of these factors should err on the safe side. Raptors provide a variety of positive values for man ranging from the aesthetic to the economic. If for no other reason than their function as indicators of the dangers of persistent toxic chemicals in the environment, they deserve to be conserved. Raptors represent an important segment of natural communities not only in their own right but also in the sense that conservation of raptors can often be expected to guarantee, as a side product, the preservation of sufficient habitat to sustain many other species that have smaller requirements in the way of space and other resources. In a political sense, the preserving of sufficient habitat for endangered and threatened raptors may prove to be the most efficient way to preserve entire avian communities.

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Water Management Practices and Their Effects on Nongame Birds in Range Habitats¹

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Abstract.--The conversion of chaparral and pinyon-juniper to desert grassland and its effects on avian habitat are examined. Numbers of species and population densities in desert shrub types are presented. The impact of manmade habitats, such as irrigation systems and urban areas, is discussed. Emphasis is placed on the extremely productive riparian ecosystems of the Southwest which are threatened by "water salvage" projects.

INTRODUCTION

The management of range habitats for wildlife in general, and nongame wildlife specifically, is a complex and too often overlooked management problem. Many factors contribute to the complexity of these problems, especially in relation to water management and habitat values.

The term "Rangeland" denotes a vast number of habitat types. When considering the dimensions included in the term one becomes involved with more than half of Dice's (1943) Biotic Province of North America, more than half of Shelford's (1945) Biomes of North America and the Lower Austral (Lower Sonoran), Upper Austral (Upper Sonoran) and to a lesser extent, Transition and even higher Life Zones of Merriam (1890). These larger units may be broken down into even smaller subunits, each with its own particular biota and associated nonbiological characteristics. These subunits have been called communities (see Odum 1959), fascinations (see Dice 1952), "vegetation types" and a myriad of other terms (see Oosting 1956). It would be impossible to treat all of the pertinent habitat types in a work of this scope. We shall emphasize the rangeland of the Southwest for it is here that water management practices are so

competitive with other range habitat values. The supplying of water for agricultural, domestic and industrial purposes is often pursued at the expense of wildlife and native habitats. Our discussion treats general watershed management practices and emphasizes the extremely productive but greatly threatened riparian (streamside) habitats.

A HISTORY OF WILDLIFE VS. GAME MANAGEMENT

As one searches the literature regarding water and habitat management practices, certain factors regarding wildlife are readily apparent. There have been two basic and extremely important problems with the historical development of the concept of "wildlife management." First has been the ignorance of principles of wildlife management or the ignoring of wildlife in general by many resource managers; and the second problem has been the academic, research, administrative and managerial confusion between the terms "game" and "wildlife."

In 1926, E. H. Clapp published A National Program of Forest Research, the work of a committee for the Society of American Foresters. This publication stands in mute evidence of the lack of concern for wildlife during the embryonic stages of resource management. Only two pages in this 232 page treatment were devoted to wildlife. These pages were largely directed toward game, predators, and rodents and their associated economic implications. In 1931, H. H. Chapman, then Harriman Professor of Forest Management in the Yale School of Forestry, published a book on Forest Management. His index

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notes three one page entries under "recreation" while wildlife is not even mentioned.

Strangely enough, it was a book on Game Management (Leopold 1933) that was one of the first to indicate an early concern for all wildlife. Aldo Leopold is considered by many as the pioneering spirit behind many of the principles of modern game management. He was keenly aware of the importance of both nongame and game species to a balanced and productive wildlife habitat. Yet, this early concern of Leopold was neither fostered nor addressed by many of his successors in forest and "wildlife" management. In the "American Forestry Series" of approximately twenty-five books, published by McGraw-Hill, the two companion volumes on "Wildlife Management" (Trippensee 1948, 1953) are solely concerned with game, fur bearers, waterfowl and fish. The index of the first volume, Wildlife Management: Upland Game and General Principals, does not even use the word "nongame" and the words "songbirds," "warblers" and "sparrows" each have a one page entry. Another well known book in the series, Stoddart and Smith's (1955) Range Management contains sections on "wildlife" which deal almost entirely with game species, rodents and predators. As recent as 1966 (Davis 1966) another text, American Forest Management, provides no treatment of wildlife. The recent periodical literature indicates only a slight improving trend. The index for the 1974 volume of American Forests (journal of the American Forestry Association) contains nine entries under the heading "wildlife." Five articles are concerned with game and/or predators, one is about the rare Kirtland's Warbler (Dendroica kirtlandii), one article is on both game and nongame species and two others only briefly mention wildlife. In the 1974 index for the Journal of Range Management, the only reference to wildlife is in regard to a book review. Even though we may disagree with the levels of priority assigned wildlife by these publications, given the socioeconomics and politics of the concerned associations, we understand much of the reasoning behind these priority levels. What is more difficult to rationalize is the persistence with which many agencies and individuals oriented toward management of wildlife resources have held to the concept of game management in place of wildlife management. Although certain taxonomic groups, e.g., the Anseriformes and ungulates, are comprised largely of game species, the term "game" is of sociological origin and not an ecological or phylogenetic derivative. In the past, most federal funding as well as that for many state wildlife agencies has been utilized for game management because of law, proclamation or convention. In many cases, the conservation

efforts that evolved in the name of game and range management were carried out at the expense of many nongame species, particularly predatory mammals and raptors (see Russo 1964). On the other hand, certain conservation efforts directed toward game species most certainly have secondary benefits that protect and perpetuate critical habitats for many nongame species of wildlife.

It is evident, that even today, much of the funding for wildlife management projects is borne by the relatively small percentage of the citizenry which engages in hunting and fishing. By virtue of this fact, the political pressures that have been directed toward the management of game species will continue and nongame wildlife species will be placed on a low priority level. If nongame wildlife research and management continue to rely on hunting and fishing groups for funding, insufficient funds will continue to contain the field of wildlife management within the narrow confines of game management. An additional problem is that wildlife management must compete with "sustained" timber yields, cattle and wool growers, and water salvage interests. Nonetheless, most federal and state agencies, which are entrusted with the protection and perpetuation of our wildlife resources, are generally directed by law to manage both game and nongame wildlife. Thus, given this mandate, the continued emphasis on game management is inconsistent with national and state charters regardless of the political and socioeconomic pressures. Examination of past work conducted with wildlife would lead one to believe that most governmental wildlife management agencies are supposed to conduct research and management programs with game, fur bearers, predators and rodents, while academicians and "conservation" groups work with the left over nongame species. However, an examination of recent publications in the wildlife management field shows an encouraging trend. The Journal of Wildlife Management is publishing an increasing number of papers on nongame species. The American Wildlife Conference transactions (published by the Wildlife Management Institute) through the years also show an encouraging tendency toward increasing concern for all wildlife, not just game species. There also appears to be a tendency for a greater understanding of the implications of habitat degradation and destruction to both game and nongame wildlife by most research organizations. In addition, many wildlife management agencies are hiring increasing numbers of nongame or general wildlife biologists. (In 1967, the Arizona Game and Fish Department was one of, if not the first agency in the United States to do so.)

Much of the recent focus on nongame wildlife is simply in response to the ever increasing non-consumptive use of our national resources by the public. A recent paper presented at the 28th North American Wildlife Conference by Cushman and McGinnis (1963) dealing with consumptive and non-consumptive public utilization of the George Washington National Forest dramatically illustrates this point. These investigators present a detailed analysis of different public activities in the National Forest. Of the 833,314 man-hours of analyzed use from June 1961 to June 1962 it was determined that more hours were spent in camping (168,614) than in hunting (140,517) and fewer hours were spent in fishing (34,119) than in sightseeing (54,395). Other non-consumptive uses included many thousands of hours spent in nature study and hiking. These findings should have raised some very pertinent questions regarding management priorities on much of our public lands.

The Wildlife Management Institute has continued to be a leader in expressing concern for all wildlife. The transactions of the 29th North American Wildlife Conference contained A. Starker Leopold's (1964) famous committee report on "Predator and Rodent Control in the United States." This report was somewhat contrary to the "established" wildlife values of that time. The transactions of the 31st conference (1966, four years before our first "Earth Day") had several papers devoted to degrading effects of pollution but the vast majority of the papers presented were still on game management. Just two years ago (1973) a technical session on Rare and Endangered Species cut across game/nongame boundaries. And, finally, in 1974, a complete session was conducted on nongame wildlife.

WATER MANAGEMENT PRACTICES, WILDLIFE VALUES AND COST-BENEFIT RATIOS

No other topic lends itself more readily to the discussion of multiple use and abuse policies than that of water management practices and habitat values. It seems incredible that man traveled along, camped and trapped on, settled in and drew water from riverine ecosystems since the beginning of history without having a better understanding of the great importance of these rivers. Historians and archaeologists have consistently pointed out the importance of rivers to civilization. We heartily agree and then use them for garbage and sewage effluent disposals, dry them up, denude them of native vegetation, turn them into canals or simply dam them. For decades, just as nongame management has been subservient to game management, other values on

watersheds have been disregarded while "water management" and salvage projects receive the principal focus. This is especially true when we review the lack of concern for maintenance of natural riparian ecosystems compared to the ever increasing concerns for supplying large metropolitan areas in the Southwest with additional water for domestic, agricultural, industrial and recreational uses.

Early settlers, particularly in the arid Southwest, considered water essential. First, drinking water was essential in sustaining life, followed by drinking water for livestock and then irrigation water was essential for raising food and cash crops. Now, little more than a century after some of the earliest settlers came to the Southwest, we find changing values and shifting usages having a profound effect on managerial priorities of resource management agencies. People have more leisure time and are demanding more and different uses of our forest, ranges, deserts and rivers; while economical emphasis has shifted from an agrarian to an industrialized technology. In Arizona, according to the Valley National Bank (1974), income from manufacturing output in 1973 was approximately double that of either the second major source of income, mineral products, or the third source, agricultural production.

Reclamation projects of the early nineteen hundreds were considered unchallengeable. The idea of an inviolate river, one which would continue running to maintain a riverine ecosystem for the enjoyment of recreationists such as campers, hikers, swimmers, fishermen, etc., was either unthought of or so low on the list of priorities it was not considered.

The Central Arizona Project, the largest project ever planned by the Bureau of Reclamation, and the associated controversy, serves as a focal point to illustrate some of the issues involved. This project, whose cost is estimated at approximately 1-1/2 to more than 3 billion dollars, would pump water uphill from the Colorado River through aqueducts for several hundred miles to storage reservoirs in central Arizona and southwestern New Mexico. A great battle has developed between those in favor of and those opposed to the CAP. Those in favor of the project claim the socioeconomic survival of central Arizona is at stake. Those opposed to the project vary from persons and groups who claim that it is economically infeasible or environmentally unsound, to those claiming that it is an insidious plot of "water salvage" agencies interested only in perpetuation of their bureaucracies.

Plans for the CAP have been known by the public for several years. It was originally planned to supply irrigation water for Arizona's central valleys. Other purposes have been proposed, e.g., recharging the subsiding underground water tables and for developing recreation (Orme Reservoir will be adjacent to the newly developed Fountain Hills, near Phoenix). In view of the forementioned shift in Arizona from an agrarian to an industrial economy the emphasis on water utilization for the CAP has also shifted to municipal and industrial usage. The Maricopa Audubon Society (in central Arizona) has recently released a pamphlet analyzing the negative effects of the four reservoirs proposed for the CAP on the paltry remains of riparian habitat in southern Arizona and southwestern New Mexico.

Water management agencies have constructed reservoir systems, canal systems, powerline networks and pipelines. They have developed vegetation-control projects on open rangeland and in forests, as well as conducting both vegetation manipulation and channelization projects along rivers and streams. Cost-benefit ratios have been established through formulae developed during decades of experience. Costs include purchase of property, construction, maintenance, interest on the principal involved and other calculable costs. Benefits include income from water and power, diminished flood losses, recreational values and other calculable benefits. Many persons and groups are beginning to question why many tangible and intangible values were not formerly estimated in cost-benefit ratios. It is the belief of some of these groups that if all wildlife and all recreational values had been used in calculating costs of some earlier and still proposed water management projects, justifications for these projects would not have been possible. Although water impoundment projects attract vast numbers of recreationists, these are not the same recreationists that utilized the area prior to its impoundment. These tangible losses (costs) could be determined by economists, but they are frequently ignored. Interestingly enough, the intangible values, although they are not calculated, are often as important or more important to the user than the tangible values. This is particularly true if wildlife could be given a "user" status. Loss of wildlife habitat and the loss of recreation derived from the presence of wildlife in their native and undisturbed habitats are intangible values that cannot be determined by either the finest economist or the most sincere water management specialist. We are not necessarily advocating a system that would evaluate all wildlife and recreational values against a gold standard. It is evident, however, that until better means

are found for validly measuring wildlife and recreational losses, input into the establishment of solid cost-benefit ratios in water management projects will be minimal.

RANGELAND HABITAT TYPES, WATER MANAGEMENT PRACTICES, AND NONGAME BIRDS

Rangeland in the United States has been traditionally considered to include the western portion of the nation, extending from the west coast to a line drawn north from central Texas through eastern Oklahoma, and including the states of Kansas, Nebraska and South Dakota (Stoddart and Smith 1955). Within this vast rangeland are a large number of distinct habitat types. Kuchler (1964) developed a widely used map for the United States that treats large vegetation types. A system for breaking these larger groups can be found in Brown and Lowe (1974a, 1974b). To analyze the water management practices and their effects on nongame birds in these habitat types we have used the vegetational classification systems of Stoddart and Smith (1955) and Lowe and Brown (1973).

Desert Shrub

Lowe and Brown (1973) divide their desert-scrub into a separate subtype for each of the four deserts in the United States. Stoddart and Smith (1955) divide this type into northern desert shrub (or intermountain shrub) and southern desert shrub. The two basic types have certain characteristics in common. As one might assume from their names, the predominant vegetation is shrubs. Rainfall in these regions is low, ground cover scant, evaporation high and grazing carrying capacity low. The desert shrub has received little water management manipulation.

Northern Desert Shrub

This is the vegetation type of the Great Basin Desert. Dominant shrubs include big sagebrush (Artemisia tridentata), other species of sagebrush (Artemisia spp.), shadscale (Atriplex confertifolia), several species of rabbitbrush (Chrysothamnus spp.), Mormon tea (Ephedra spp.) and other shrub species. In contrast to the southern desert shrub, much of the precipitation falls as snow and dry conditions, combined with short growing seasons, probably contribute to the low species diversity and population densities found in bird species. Balph (1973) reported approximately 80 birds per 100 acres on shrub plots at the Curlew Valley Validation Site (United States International Biome Program). One plot, in a grassland subtype, had only one nesting species, the Horned Lark (Eremophila alpestris). Some of our preliminary work in northern Arizona indicates

a high correlation between grazing (especially with sheep) and paucity of bird populations.

Southern Desert Shrub

This vegetation type encompasses the Mohave, Sonoran and Chihuahan Desert lowlands. Some of the lowest rainfall (3-12 inches or less per year), highest temperatures (100-120 degrees Fahrenheit or higher in summer) (Green and Sellers 1964) and highest evaporation rates (100-140 inches or more per year) occur in these southern lowlands. From an aesthetic standpoint, these deserts, especially the Sonoran desert, are greatly admired. Native vegetation includes creosotebush (Larrea divaricata), tarbush (Flourensia cernua), several species of cacti (family Cactaceae) including the sahuaro (Cereus gigantea), several legumes which develop into large shrubs or small trees, e.g., mesquite (Prosopis spp.), catclaws (Acacia spp.) and paloverde (Cercidium spp.).

Although grazing is a common practice throughout much of this type, the vast grazing area needed to raise livestock (100 to several hundred acres per cow) is rendering the economic feasibility of these grazing operations questionable. Stoddart and Smith (1955) state, "Because of unfavorable growth conditions, the southern desert shrub probably never has been a productive rangeland, but at present it is materially lower than originally." Hastings and Turner (1965) have recently documented the decline in range conditions over much of this area.

Due to the low water yield potential of this desert type, water management practices in these areas have been minimal except in the riparian type (see discussion under Riparian Habitat). Clearing of shrubs and small trees prior to leveling land for irrigation has probably been the major activity. In areas where irrigation has been practiced for several decades a definite shift in bird species and population numbers has occurred (Johnson 1972). It has been demonstrated (MacArthur and MacArthur 1961) that for most habitat types plant species composition has no correlation with bird species composition. For the southern desert shrub, however, Tomoff (1974) has demonstrated that the breeding birds are highly responsive to particular life forms. Should water management practices or other forms of vegetational manipulation be considered in this habitat type, an evaluation of its impact on breeding birds may be determined by reviewing Tomoff's (1974) paper.

Breeding bird densities in southern desert shrub vary from 10 to over 100 pairs per 100

acres depending upon the specific habitat (see Dixon 1959; Hensley 1954; and Raitt and Maze 1968). Throughout the Southwest, many of the large metropolitan areas have developed in the southern desert shrub. The impact this urbanization has had on bird life is phenomenal. Emlen (1974) found an estimated 1230 birds per 100 acres in an urban area in Tucson, Arizona, compared to 46.7 birds per 100 acres in a desert area approximating the original urban area vegetation type. Emlen (1974) attributed much of the difference to the greater availability of water and seeds in the urban area.

Grassland

This vegetation type may be divided into four major subtypes: the desert grassland, mountain grassland, plains grassland and palouse grassland.

The most xeric type, the desert grassland, is often called mesquite grassland, yucca grassland, pinyon-juniper grassland or oak grassland. This type is typically restricted to the southwestern United States and northern Mexico. Rainfall is generally less than 20 inches per year (U.S.D.A. 1941) with evaporation rates as high as 80 inches or more per year (Stoddart and Smith 1955). Due largely to arid conditions and inability of the higher quality forage grass species to recover from overgrazing, this type is the least suited for grazing. Several experimental ranges (such as the Santa Rita Experimental Range in southern Arizona and the Jornada Experimental Range in southern New Mexico) have been set aside for investigating the effects of various grazing practices in this vegetation type (see Martin and Reynolds 1973 for extensive review of desert grassland literature).

Water management practices in this habitat type have consisted of both mechanical and chemical controls of mesquite, (which reach unnaturally high densities on overgrazed rangeland) (Humphrey 1962), and other invading species, in order to increase water yield and forage protection.

Bird densities recorded by Russell et al. (1972) on the Santa Rita Experimental Range were relatively low, with 10 species making up a total population of 69 pairs per 100 acres.

The mountain grassland is associated with the coniferous forest vegetation type and is commonly found in clearings as mountain meadows. Since another section of this symposium deals with the coniferous forest we shall not deal with this vegetation type.

Table 1.--Taxa involved in recent hybridization on the Great Plains

<u>Eastern Species</u>	<u>Western Species</u>	<u>New Name</u> ^{1/}
Yellow-shafted Flicker (<u>Colaptes auratus</u>) (Short 1965) ^{2/}	Red-shafted Flicker (<u>Colaptes cafer</u>) AND Gilded Flicker (<u>Colaptes chrysoides</u>)	Common Flicker (<u>Colaptes auratus</u>)
Baltimore Oriole (<u>Icterus glabula</u>) (Rising 1970; Sibley and Short 1964) ^{2/}	Bullock's Oriole (<u>Icterus bullockii</u>)	Northern Oriole (<u>Icterus glabula</u>)
Rose-breasted Grosbeak (<u>Pheucticus ludovicianus</u>) (West 1962) ^{2/}	Black-headed Grosbeak (<u>Pheucticus melanocephalus</u>)	No change
Indigo Bunting (<u>Passerina cyanea</u>) (Sibley and Short 1959) ^{2/}	Lazuli Bunting (<u>Passerina amoena</u>)	No change

^{1/} With the publication of the Supplement to the A.O.U.'s Check-list (1973) this is the new name to be used for both eastern and western members of the group as well as any "hybrids."

^{2/} Papers which analyze hybridization in these species.

In native plains and palouse grassland habitat types the effects of water management practices on nongame bird habitats are negligible. Wiens (1974) gives an excellent review of bird populations in these grassland types.

Shelter Belts and Nongame Birds

During the earlier 1900's a greatly encouraged conservation practice in the Great Plains was the planting of trees and shrubs as windbreaks, cover for wildlife, for fruit production and ornamental purposes. Available water was also increased through associated irrigation systems. These trees and shrubs, as well as utility poles and transmission lines, have provided avenues by which certain species of birds move back and forth between the eastern deciduous hardwood forests and western tree and shrub types. Thus, the standard grassland avifauna, containing such species as Lark Buntings (Calamospiza melanocorys), Horned Larks (Eremophila alpestris) and Meadowlarks (Sturnella spp.), has been augmented by tree dwelling species such as the Eastern Kingbird (Tyrannus tyrannus) moving west and the Western Kingbird (Tyrannus verticalis) moving east. In addition we suspect that the increased sightings in the west of certain eastern species such as the Roughlegged Hawk (Buteo lagopus) may be due to this phenomenon.

With the retreat of glaciers from central North America after the Pleistocene there was an increase in grasslands (Martin 1958). One of the largest of these grasslands, the Great Plains, developed to serve as an effective barrier separating the forests and shrub lands of the east from those of the west. Certain closely related plant and animal species were thus effectively isolated from one another. When European man settled these grasslands and planted islands of trees and shrubs a means of secondary contact was established for many of these closely related species. Thus, several bird species which had been considered distinct species (A.O.U. 1957) hybridized freely when individuals from the eastern "species" of the genus encountered members of the western "species" of the genus in this newly created habitat.

Table 1 shows taxa originally considered distinct species but now considered subspecies by many ornithologists. In addition to these taxa, which were previously considered species, certain eastern and western subspecies that were originally separated by the Great Plains, such as in the Rufous-sided Towhee (Pipilo erythrophthalmus) (Sibley and West 1959) are now interbreeding. Therefore, man has interfered with distribution and isolation of incipient species and thus with evolution itself.

Chaparral

Chaparral is composed largely of evergreen sclerophylls such as scrub oak (Quercus turbinella and other species), mazanita (Arctostaphylos spp.), deer or buckbrush (Ceanothus spp.) and in California, chamise (Adenostoma spp.). Stoddart and Smith (1955) divide chaparral into three subtypes:

(a) California chaparral, occurring in extensive stands on the hills and flanks of mountains in southern California; (b) oak scrub, found in the foothills of the Rocky Mountains and Inter-mountain region (vast areas of this type are composed largely of gambel oak (Quercus gambelii); and (c) mountain brush, occurring in the elevations between the desert grassland and coniferous forests of the Southwest.

Certain edaphic and climatic attributes of the three subtypes are quite different, however, most of the basic characteristics are so similar in regards to water management and habitat values, that we shall treat it all as one basic type. Chaparral has been considered by many to be an undesirable vegetation type. The major management practices have consisted of trying to control or eradicate chaparral and usually to convert it to grass. Control is commonly by mechanical means (e.g., root plowing and burning) or by herbicides. Certain species of wildlife, including nongame birds, utilize chaparral quite heavily, but we know of no obligate chaparral species other than possibly the Wrentit (Chamaea fasciata), a California species belonging to a monotypic family (Bent 1948; Dawson 1923). Some of our research suggests that blocks of chaparral interspersed with other vegetation types, (commonly desert grassland or pinyon-juniper) may be more conducive to increases in nongame bird species diversity. Root plowing, to partially open dense stands of chaparral on the Prescott National Forest, apparently increased bird usage, possibly due to the "edge effect" (Loe and White 1972). A project conducted by Johnson^{4/} on the Sycamore Canyon watershed found little difference in total numbers of bird species in the areas that had undergone chaparral control in comparison to unmanipulated plots, and frequent clearings or patches of different vegetation (e.g., cypress (Cupressus glabra) or ponderosa pine (Pinus ponderosa)) occur throughout the unmanipulated plots. Many persons interested in grazing and water salvage continue to advocate chaparral control. However, its value in wildlife management needs to be

^{4/} Johnson, R. R. 1973. The effects of chaparral control on birds of the Mazatzals, Maricopa Co., Arizona. Rpt. to Rocky Mt. Forest and Range Exper. Sta., Tempe.

better assessed. Almost all work done to date on chaparral management in relation to wildlife habitat has been with game species (see synopsis in Hibbert et al. 1974). An economic analysis of chaparral conversion to grass was recently published by Brown et al. (1974). The vegetation on 59 percent (850,000 acres) of the land managed by the Forest Service in the 8.4 million acre Salt-Verde Basin consists of chaparral. This analysis found conversion to be economically beneficial on some plots but not on others. Nongame wildlife values were seldom considered in actual cost-benefit ratios.

Pinyon-juniper

This habitat type is characterized by combinations of several species of pinyons (Pinus edulis and allies) as well as junipers (Juniperus spp.). Other names applied to this woodland type are juniper-pinyon (Lowe and Brown 1973) and pigmy forest. This vegetation type is widely distributed throughout the western United States. It generally grows where rainfall is approximately 12 to 18 inches a year and evaporation rates and growing seasons are similar to areas where desert and short grass occur (U.S.D.A. 1941; Stoddart and Smith 1955). These species commonly grow in shallow, rocky soils with low organic content and/or on steep slopes with poor to medium ground cover. Certain species, especially junipers, occur in grasslands as patches on rocky areas and among cliffs and canyons ("juniper breaks").

The pinyon-juniper type is found growing in a vast array of contrasting situations. It commonly occurs at elevations between the desert shrub types and coniferous forest, often starting in the desert grass and continuing upward in elevation in association with chaparral, oak and pine-oak woodland. No other type, beside chaparral and riparian vegetation, has received so much concern regarding water management practices from cattle and irrigation interests. This vegetation type has been the object of intense efforts to convert it to grassland. Control efforts have consisted mainly of chaining (pulling a chain or cable between large tractors, in effect "mowing the trees down") and bulldozing. Salt River Project officials claim increased water yields after conversion (pers. comm.) and the number of cattle which can be supported increases on some ranges after conversion, according to some ranchers and Forest Service officials (pers. comm.). Reynolds (1972) and Clary et al. (1974) discussed the effects of some of these conversion projects on wildlife habitat.

As with the chaparral, very few investigations have been conducted with nongame

wildlife in this habitat type. Some of our censuses indicate that patches of pinyon-juniper growing with desert grass, chaparral or ponderosa pine are relatively productive. Table 2 shows the number of species found on different plots in pinyon-juniper, chaparral and converted desert grassland habitat (Douglas and Johnson 1972).

In summation, recent cost-benefit studies show that pinyon-juniper removal is questionable and often does not increase water yields (Clary et al. 1974). Folliott and Thorud (1974) present information showing that most vegetation projects below the elevation of coniferous forests are questionable.

Riparian Habitats

Water management practices have had, and are continuing to have their greatest impact on nongame birds in the riparian habitats of the southwestern United States. To illustrate this we shall briefly review some of the more extensive water management projects and habitat damage on the major drainages of Arizona and New Mexico.

The Gila River originates as a small stream in the mountains of southwestern New Mexico and flows southwest approximately 55 miles before entering Arizona. In Arizona, the river develops into a major system, draining more than 14,000,000 acres. Originally, the river flowed more than 500 miles into and across Arizona to the Colorado River near the

Mexican boundary. Today, the lower two-thirds of the river from Coolidge Dam (San Carlos Reservoir) downstream to its confluence with the Colorado is dry. Remnants of the vast original riparian forests, mesquite woodlands and miles of sloughs and marshes documented in the writings of early explorers (Emory 1848) are practically nonexistent. The paltry remains of riparian habitat still existing in these areas are largely maintained by sewage effluent, e.g., areas west of Phoenix, or tail water and underground seepage from irrigation, e.g., in the Welton-Mohawk Irrigation District. The upper third of the river (above Coolidge Dam) supports some of the finest riparian habitat remaining in the Southwest today. Along this portion of the river both game and nongame birds have been studied by several recent investigators (Hubbard 1971; Johnson et al. 1973^{5/}; and Zimmerman 1970^{6/}).

The Gila River Valley of New Mexico and the adjacent Gila Wilderness is one of the most extensively studied sections of the river. In

^{5/} Johnson, R. R., S. W. Carothers and D. B. Wertheimer. 1973. The importance of the lower Gila River, New Mexico, as a refuge for threatened wildlife. Museum of Northern Arizona. Unpublished manuscript.

^{6/} Zimmerman, D. A. 1970. Birds and bird habitation on National Forest lands in the Gila River Valley, southwestern New Mexico. Western New Mexico University and Gila National Forest, Silver City. Unpublished manuscript.

Table 2.--Number of species of birds on 10 acre study plots in pinyon-juniper woodland.^{1/}

CLASSIFICATION	Pinyon-juniper	P-j/ Grass	P-j/ newly cleared	P-j/ old clearing	Mixed P-j/ chaparral	P-j streamside (Inter- mittent)	(Perma- nent)
Breeding Species	7,6,10,11	13	5	10	9,16,16	20	41
Summer Visitants	7,4, 6, 2	5	3	6	9, 3, 3	3	10
Summer Species	14,10,16,13	18	8	16	18,19,19	23	51
Migrants and Wintering	10, 9,12, 7	19	3	14	22,10,26	18	24

^{1/} Each number is for a 10 acre plot censused regularly and equally during 1971 and 1972. Thus, there were 4 pinyon-juniper plots, 1 pinyon-juniper grassland plot, 1 pinyon-juniper newly cleared plot, etc.

addition to supporting an extremely diverse avifauna, this area also supports one of the most diverse raptor breeding populations known today in the Southwest. Nesting raptors include the Black Hawk (Buteogallus anthracinus), Zone-tailed Hawk (Buteo albonotatus), Prairie Falcon (Falcon mexicanus), allegedly, Bald Eagles (Haliaeetus leucocephalus), Peregrine Falcons (Falco peregrinus) and formerly, Gray Hawks (Buteo nitidus). The effects of human activities on some of these rare species have been discussed by Hubbard (1965) and Zimmerman (1965). In spite of the studies done on this area, information regarding population densities, social organization and feeding relationships within the avian community is practically nonexistent.

The Salt River, a major tributary of the Gila, draining approximately 6,900 square miles of east-central Arizona supported more riparian habitat in historic times than it does now. The upper half of the river is relatively wild, but the narrow canyons through which it flows are not wide enough to support substantial riparian forests. The lower reaches of the river have dried up due to upstream dams. Sections of the middle segment of the river, which are now submerged by four irrigation storage reservoirs, originally supported extensive riparian habitat. Remains of this habitat can still be seen when the water levels in these reservoirs are low. Thus, the only remaining segment of the original cottonwood forest and extensive mesquite woodlands along the entire Salt River occur in the approximately 10 mile long floodplain between Stewart Mountain Dam and the Granite Reef Diversion Dam. Many of the more important bird records for the Salt River Valley are from this area (Johnson and Simpson 1971). It may be the only area left along the entire Salt River where obligate riparian species find suitable nesting resources. Unfortunately, this last remaining native riparian area is proposed for inundation by Orme Reservoir under the Central Arizona Project.

The Verde River, a major tributary of the Salt River, originates in central Arizona and flows southward for more than 100 miles. It drains more than 7,000 square miles of some of the finest central Arizona rangeland. Portions of the Verde River riparian habitat have been the focal point for some rather extensive phreatophyte control projects. These projects were directed toward the almost total removal of the native riparian habitat in selected areas throughout the drainage.

Through studies sponsored by the Arizona Department of Game and Fish and the Coconino National Forest, we have recently investigated breeding bird populations and avian community

response to vegetative management practices throughout the Verde River and its tributaries. Our results serve to document that the riparian habitats of the system support some of the most productive avian aggregations ever reported in North America. These studies also demonstrate that certain governmental and privately sponsored habitat management practices directed toward water salvage and flood control (i.e., phreatophyte control) and increased exploitation of the riparian habitat for urbanization, agriculture and grazing have devastating effects on the avian productivity.

Riparian habitats in arid environments are not only unique in terms of total avian productivity and certain physiognomic patterns which affect avian social organization (Carothers et al. 1974), but we must also emphasize the importance of the habitats to the survival of a large number of southwestern bird species. We have documented that over 50 percent of the species breeding in homogeneous cottonwood (Populus fremontii) stands along the Verde River and its tributaries are exclusively dependent upon this habitat for reproduction. Our studies indicate that there is not another habitat type in North America that is as important to a similarly large aggregation of non-colonial nesting bird species. In the riparian habitat dozens of species may be named, many of them relatively common species, that would face certain extirpation in the event of total loss of the riparian vegetation.

To illustrate the effects of phreatophyte control on avian densities on some riparian areas, particularly the homogeneous cottonwood type, we shall here briefly summarize a portion of the results of five years of intensive investigations on the breeding birds of the Verde Valley. For a complete review of our methodology and vegetative descriptions of the study plots see Carothers et al. (1974). All study sites were selected for their similarities in age class of trees, proximity to water, general topography and physiognomic features. The only major apparent difference in these study sites was the number of trees per acre. Two of the areas had been subjected to varying degrees of phreatophyte control while the third "unmanipulated" area served as a control. When these investigations were initiated in 1969, the control plot contained 46.6 trees per acre. In five years, this has been reduced to 38.3 trees per acre through manipulative practices of private landowners by cutting of trees for use in fuel wood and fence posts. The two manipulated plots, Area 2 and Area 3 had been reduced to 26.0 and 10.3 trees per acre respectively. Table 3 illustrates the differences in breeding bird densities found on these study plots.

Table 3.--Average breeding bird densities found on manipulated vs. unmanipulated homogeneous cottonwood riparian study plots (1969-1973).

Study Plot	Tree Density per Acre	Breeding Bird Density Pairs per 100 acres
Control	46.6 (38.3) ^{1/}	1058.8 (605.2) ^{2/}
Area 2	26.0	758.4
Area 3	10.3	484.3

^{1/} After 1971, the area had been reduced to 38.3 trees per acre.

^{2/} 605.2 pairs per 100 acres reflects the average density for the two years after the control area had been disturbed.

Although the relationships of bird communities to riparian habitats are varied and complex (see Carothers et al. 1974) these data summarizations very dramatically demonstrate that phreatophyte control in mature native riparian habitats has a negative effect on breeding bird populations. The bird species are obviously responding to the presence or absence of certain vegetational parameters associated with the foliage produced by the riparian growth. What we have not yet adequately established, however, is how low the tree densities can go before a significant portion of the total avian community is extirpated. Based on preliminary observations, the population densities of the breeding birds begin to decline even more rapidly than we have thus far indicated when the tree density falls below 10 trees per acre.

SUMMARY AND CONCLUSIONS

We have discussed the impact of water management practices on bird habitat and consequential effects on numbers of species (alpha diversity) and population densities found in various habitat types. Although our emphasis has been on nongame birds we would emphasize that when one conducts a research or management project on a given habitat he must be concerned equally with both game and nongame species. Birds do not recognize the sociological distinction between "game and nongame" but they do recognize changes in habitat.

Of the range habitats discussed, the grasslands have probably been most modified by man and his domestic herbivores. Species diversity and population densities discussed in this paper indicate low numbers for the range habitats when compared with western coniferous forests (Carothers et al. 1973) or eastern deciduous

hardwood forests.^{7/} Urban situations in the southern desert shrub often support populations several times that of the original native habitat.

The greatly endangered riparian habitats are discussed with the effects of "water management and salvage" projects on this critical habitat type. The highest population densities for non-colonial nesting birds in North America are recorded for this type (Johnson 1970). We feel that an awareness by the majority of the American public rather than pressure by consumptive minorities encouraged the Public Land Law Review Commission (1970) to write, "The Federal Government has a responsibility to make provision for protecting, maintaining and enhancing fish and wildlife values on its lands generally because of the importance of those values as part of the natural environment over and above their value for hunting, fishing and other recreational purposes." We see encouraging signs that resource managers are accepting and implementing this challenge.

RECOMMENDATIONS

1. The riparian habitat should be managed as the most sensitive and most productive North American habitat. This is especially important since certain other uses are highly competitive for the water on which this type is dependent.

2. Emphasize the importance of wildlife habitat in land use planning as strongly as alternative uses. The degree of importance that wildlife now occupies can be gathered in part from the amount of literature published. For example, while approximately 5,000 abstracts

^{7/} Refer to session on Deciduous Forest Habitats, this Symposium.

are published annually in Wildlife Review (U.S.D.I., Fish and Wildlife Service) more than 15,000 abstracts are published annually in Selected Water Resources Abstracts (U.S.D.I., Water Resources Scientific Information Center).

3. Develop methods for determining wildlife and recreational values to provide for better input into the cost-benefit studies determining the best usage for a given area.

4. Conduct projects to determine the following:

a. The minimum allowable area and configuration for a particular habitat type before the loss of wildlife species occurs.

b. The maximum distance which can separate islands of a given habitat type before the loss of species occurs.

c. Both optimal and minimal requirements within a given habitat type, such as trees per acre, foliage volume, ground cover, etc.

Determining these factors may be the most important problem facing us today. All the "threatened species recovery teams" we can possibly amass will not prevent many species from becoming extinct in their native habitat if we degrade their habitats past the point of no return.

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Discussion

MR. MORRIS: I sense a difference of opinion in the matter of diversity of habitat and the size of habitat units. I would like to mention specifically a problem associated with control of sagebrush and reseeding with crested wheatgrass. We are talking about areas where 10,000 or more acres in one great block were sprayed and then seeded to crested wheat. We urged the BLM to cut down the size of these blocks to make them linear instead of rectangular and to provide more edge. Were we wrong?

MR. BUTTERY: I believe that by breaking up large blocks of sagebrush, diversity of bird species will likely be increased. But diversity should be judged on the basis of quality as well as quantity.

MR. WIENS: The optimum area to plant crested wheatgrass for populations of nongame birds

would be zero. Birds simply don't use it to any degree.

MR. GROVE: As Dr. Wiens pointed out, it's not diversity per se; it's maintaining natural communities that counts. I would propose the use of indicator species. I use the example of the mountain plover, which is a very good indicator species for blue grama-buffalo grass prairie. The mountain plover occurs in those areas that are subjected to heavy summer grazing. In tall grass prairie the upland plover and greater prairie chicken are indicators of low grazing intensity.

MR. WIENS: I think it points out the fact that through rangelands there are a number of species assemblages; that one cannot stipulate a certain grazing level that will work throughout rangelands.

Thursday Morning, May 8

Management of Coniferous Forest Habitats

*Presiding: G. A. Swanson
Colorado State University*



Avian Communities, Energetics, and Functions in Coniferous Forest Habitats¹

John A. Wiens^{2/}

Abstract.--North American coniferous forests contain relatively rich breeding avifaunas. Censuses taken in 5-25 ha plots record 6-32 breeding species, with the "richest" avifaunas occurring in Northeastern, Southeastern, and Sierra Nevada forests. On the average, 17-27 percent of all individuals present in a plot belong to the single most abundant ("dominant") species; these species are frequently broadly distributed over North American coniferous forest regions. Breeding densities in various forest regions average 329-1456 individuals/km², while standing crop biomass averages 65-283 g/ha; values are greatest in Pacific Northwest forests, and lowest in immature stages of Northeastern forests. In most regions, there are substantial annual variations in avian density and biomass. Ecologically, foliage-feeding insectivores overwhelmingly dominate the avifaunas of forests in the Northeast, Southeast, and North, but their proportionate contribution to density and biomass decreases toward the west and Northwest. In many Northeastern forests, more than half of the individuals present in a stand are warblers, while in most western forests less than 10 percent of the individuals are warblers.

Energy flow through breeding avifaunas in western Oregon coniferous forests varies from 10.5 to 20.8 Kcal m⁻² breeding season⁻¹. Roughly 80 percent of the energy flow is obtained from animal prey, chiefly foliage insects. Consumption of foliage insects and seeds may constitute a major functional role of birds in forest ecosystems, especially in relation to pest insect population dynamics and to reforestation processes.

INTRODUCTION

The mention of coniferous forests may evoke a wide array of images to the layman: foggy groves of towering redwoods, immense sequoia, scrubby jackpine expanses, orderly pine plantations, and so on. Superimposed on this natural array of coniferous forest communities are various disturbances, such as burns, clear-cuts or insect outbreaks. These various forces act to produce a broad spectrum of

coniferous forest "types", so that it becomes difficult to produce generalizations which pertain throughout such communities. Nonetheless, when one considers the populations of nongame bird species occupying such habitats, there is a general impression that the avifauna is diverse, with small, secretive, canopy-dwelling species predominating, complimented by a smaller set of "trunk-feeders", such as woodpeckers and nuthatches.

But such broad qualitative impressions are of limited use to the land manager who must establish policies for management of such habitats consistent with the well-being of nongame bird populations. Ideally, policies should be founded on a thorough knowledge of the biological attributes and interrelationships of the populations of all important species. We possess such information, however, for few coniferous forest bird populations. Thus land

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management decisions must be made from a less detailed foundation: information on the occurrence of different species in coniferous forests, on patterns of organization in the avian communities, on the energetic and trophic linkages of birds to the forest, on the roles birds may play in the "functioning" of coniferous ecosystems, and on the stability or resiliency of coniferous avifaunas---their sensitivity to habitat alterations.

In this paper I address aspects of these points, within a rather general framework. I emphasize breeding communities, not because they are most important in coniferous habitats (there are compelling reasons to think otherwise; see Fretwell 1972), but because little information is available from other seasons. I address primarily avian community patterns rather than single species characteristics, believing the former to be more instructive in the context of this symposium. Likewise, I dwell little upon theoretical aspects of community structure, such as niche relationships, competitive regimes, optimization strategies, etc. (see Cody 1974, Karr 1971), since a more descriptive synthesis may be of greater immediate utility. I have omitted quail and grouse (Galliformes), raptors (Falconiformes) and large Corvids (e.g., Crows, Ravens) from my considerations because they are not normally censused with any degree of reliability in avian community censuses. Finally, I make no claim to have surveyed all of the literature relating to coniferous forest bird communities; hopefully no critical studies have been omitted, and the generality of any conclusions which do emerge will not be destroyed by the omission of some censuses. With these disclaimers in mind, we may consider some attributes to nongame bird (primarily passerine) breeding communities in coniferous forests of North America.

THE AVIFAUNA

The Data Base.

This analysis is based upon breeding censuses conducted over a wide range of coniferous forest situations in North America, primarily during the last decade or two. Most of these censuses were conducted using spot mapping techniques (Enemar 1959, Svensson 1970) or similar techniques. Census plots were variable in size, but generally ranged from 5-25 ha. In all, over 130 breeding censuses formed the foundation for this review. The locations of these censuses are depicted in figure 1 in relation to the distribution of major elements of coniferous forests in North

America. Specific information on these census locations is given in Appendix I. It would be convenient for analysis to assign these different censuses to different expressions of coniferous forest habitats. There is so much local variation in the plant composition and structure of coniferous forests, however, that assignment of individual censuses or census locations to particular habitat types becomes quite difficult. As an alternative, I have based the following analyses on geographical subdivisions of coniferous forests in North America. These divisions, which are also shown in figure 1, are of course arbitrary, but do agree in a very general sense with some major variations in coniferous forest habitats in North America. Northwest coastal coniferous forests, for example, are certainly distinctly different from those characterizing the Rocky Mountains, and those of Southeastern United States differ markedly in vegetational composition and environments from those of northern Canada (the so-called "boreal" forests). Detailed classifications of coniferous forest types within the United States are given by K  chler (1964).

The analyses based upon the coniferous forests "regions" of figure 1 must be considered as very general. The reader interested in more specific information on avian community organization and species composition within these regions should consult the tabulated census results given in Appendix I and the original references there cited. I have supplemented the analyses of coniferous forest avifaunas based upon these North American censuses with information from other parts of the world (mostly Europe) where appropriate, in order to place the North American results within a broader perspective.

Species Distribution Patterns

While most of this analysis is based upon community rather than single species attributes, it is nonetheless important to document in at least a general way the patterns of distribution of some of the major species of North American coniferous forests. A total of 148 species are represented in the breeding censuses of coniferous forests included in this review (table 1). To some degree, this large number of component species stems from the broad distributional spread of coniferous forests over the North American continent, since forests characterizing given regions within North America contained substantially fewer species. The greatest number of species was recorded in Northeastern mature coniferous forests, and the smallest number in "immature" coniferous forests in this same region. Over other regions of North America the total number of species recorded was relatively uniform, with the exception of the lower species count in the forests of the Sierra Nevadas of



Figure 1.--Locations of breeding bird censuses included in this review. The hatched areas approximate the distribution of coniferous forest habitats in North America. Numbers refer to the census locations given in Appendix I. The inset indicates how census locations were grouped for the purposes of this paper: NE=Northeastern, SE=Southeastern, N=Northern, RM=Rocky Mountain, SN=Sierra Nevada, NW=Northwest coastal.

Table 1--Species recorded in breeding censuses of various coniferous forest regions of North America (figure 1). Values are percentages of censuses (N) in which the species was recorded; parenthetical values indicate the percentages of censuses in which the species attained dominance.

Species	Sample Size:	Coniferous Forest Region					
		Northeast	Northeast	Southeast	Northern	Rocky	Sierra
		Immature	Mature			Mountain	Nevada
		12	22	11	15	22	16
							29
Band-tailed Pigeon	-	-	-	-	-	-	38
(<i>Columba fasciata</i>)	-	-	-	-	-	-	(0)
Mourning Dove	-	5	36	-	27	-	10
(<i>Zenaidura macroura</i>)	-	(0)	(0)	-	(0)	-	(0)
Yellow-billed Cuckoo	-	5	-	-	-	-	-
(<i>Coccyzus americanus</i>)	-	(0)	-	-	-	-	-
Black-billed Cuckoo	-	5	-	-	-	-	-
(<i>Coccyzus erythrophthalmus</i>)	-	(0)	-	-	-	-	-
Ruby-throated Hummingbird	-	-	27	-	-	-	-
(<i>Archilochus colubris</i>)	-	-	(0)	-	-	-	-
Broad-tailed Hummingbird	-	-	-	-	36	-	-
(<i>Selasphorus platycercus</i>)	-	-	-	-	(0)	-	-
Calliope Hummingbird	-	-	-	-	-	19	-
(<i>Stellula calliope</i>)	-	-	-	-	-	(0)	-
Rufous Hummingbird	-	-	-	-	-	-	10
(<i>Selasphorus rufus</i>)	-	-	-	-	-	-	(0)
Allens Hummingbird	-	-	-	-	-	-	21
(<i>Selasphorus sasin</i>)	-	-	-	-	-	-	(3)
Common Flicker	17	45	45	40	36	94	24
(<i>Colaptes auratus</i>)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
Pileated Woodpecker	-	14	9	13	5	31	14
(<i>Dryocopus pileatus</i>)	-	(0)	(0)	(0)	(0)	(0)	(0)
Red -bellied Woodpecker	-	-	55	-	-	-	-
(<i>Centurus carolinus</i>)	-	-	(0)	-	-	-	-
Acorn Woodpecker	-	-	-	-	-	-	10
(<i>Melanerpes formicivorus</i>)	-	-	-	-	-	-	(0)
White-headed Woodpecker	-	-	-	-	-	69	-
(<i>Dendrocopus albolarvatus</i>)	-	-	-	-	-	(0)	-
Yellow-bellied Sapsucker	8	27	-	40	5	88	17
(<i>Sphyrapicus varius</i>)	(0)	(0)	-	(0)	(0)	(0)	(0)
Williamson's Sapsucker	-	-	-	-	23	25	-
(<i>Sphyrapicus thyroideus</i>)	-	-	-	-	(0)	(0)	-
Hairy Woodpecker	-	32	45	47	36	88	66
(<i>Dendrocopus villosus</i>)	-	(0)	(0)	(0)	(0)	(0)	(0)

		Coniferous Forest Region						
Species		Northeast Immature	Northeast Mature	Southeast	Northern	Rocky Mountain	Sierra Nevada	Northwest Coastal
	Sample Size:	12	22	11	15	22	16	29
Downy Woodpecker (<i>Dendrocopus pubescens</i>)		-	23	27	-	-	-	17
		-	(0)	(0)	-	-	-	(0)
Black-backed Three-toed Woodpecker (<i>Picoides arcticus</i>)		8	14	-	-	14	38	3
		(0)	(0)	-	-	(0)	(0)	(0)
Northern Three-toed Woodpecker (<i>Picoides tridactylus</i>)		8	-	-	-	-	-	-
		(0)	-	-	-	-	-	-
Eastern Kingbird (<i>Tyrannus tyrannus</i>)		8	9	-	-	-	-	-
		(0)	(0)	-	-	-	-	-
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)		-	27	45	-	-	-	-
		-	(0)	(0)	-	-	-	-
Eastern Phoebe (<i>Sayornis phoebe</i>)		-	5	-	-	-	-	-
		-	(0)	-	-	-	-	-
Yellow-bellied Flycatcher (<i>Empidonax flaviventris</i>)		25	32	-	27	-	-	3
		(0)	(0)	-	(0)	-	-	(0)
Acadian Flycatcher (<i>Empidonax virescens</i>)		-	-	36	-	-	-	-
		-	-	(0)	-	-	-	-
Least Flycatcher (<i>Empidonax minimus</i>)		-	-	-	40	-	-	-
		-	-	-	(0)	-	-	-
Alder Flycatcher (<i>Empidonax trailii</i>)		-	-	-	20	-	-	-
		-	-	-	(0)	-	-	-
Hammond's Flycatcher (<i>Empidonax hammondi</i>)		-	-	-	7	27	38	14
		-	-	-	(0)	(0)	(0)	(0)
Dusky Flycatcher (<i>Empidonax oberholseri</i>)		-	-	-	-	5	63	7
		-	-	-	-	(0)	(6)	(0)
Western Flycatcher (<i>Empidonax difficilis</i>)		-	-	-	-	5	-	76
		-	-	-	-	(0)	-	(10)
Eastern Wood Pewee (<i>Contopus virens</i>)		-	36	55	13	-	-	-
		-	(0)	(0)	(0)	-	-	-
Western Wood Pewee (<i>Contopus sordidulus</i>)		-	-	-	-	36	69	28
		-	-	-	-	(14)	(19)	(0)
Olive-sided Flycatcher (<i>Nuttallornis borealis</i>)		-	9	-	-	23	56	28
		-	(0)	-	-	(0)	(0)	(0)
Violet-green Swallow (<i>Tachycineta thalassina</i>)		-	-	-	-	5	-	7
		-	-	-	-	(0)	-	(0)

Species	Coniferous Forest Region						
	Northeast Immature	Northeast Mature	Southeast	Northern	Rocky Mountain	Sierra Nevada	Northwest Coastal
Sample Size:	12	22	11	15	22	16	29
Tree Swallow (<u>Iridoprocne bicolor</u>)	8 (0)	- -	- -	- -	5 (0)	- -	3 (0)
Blue Jay (<u>Cyanocitta cristata</u>)	8 (0)	68 (0)	91 (0)	40 (0)	- -	- -	- -
Steller's Jay (<u>Cyanocitta stelleri</u>)	- -	- -	- -	- -	9 (0)	75 (0)	76 (0)
Gray Jay (<u>Perisoreus canadensis</u>)	8 (0)	18 (0)	- -	53 (0)	18 (0)	- -	14 (0)
Clark's Nutcracker (<u>Nucifraga columbiana</u>)	- -	- -	- -	- -	27 (15)	- -	- -
Black-capped Chickadee (<u>Parus atricapillus</u>)	8 (8)	86 (0)	45 (0)	20 (0)	5 (0)	- -	7 (0)
Carolina Chickadee (<u>Parus carolinensis</u>)	- -	- -	55 (0)	- -	- -	- -	- -
Mountain Chickadee (<u>Parus gambeli</u>)	- -	- -	- -	- -	73 (18)	100 (13)	- -
Boreal Chickadee (<u>Parus hudsonicus</u>)	58 (0)	23 (0)	- -	33 (0)	- -	- -	- -
Chestnut-backed Chickadee (<u>Parus rufescens</u>)	- -	- -	- -	- -	- -	- -	90 (28)
Tufted Titmouse (<u>Parus bicolor</u>)	- -	- -	55 (0)	- -	- -	- -	- -
Common Bushtit (<u>Psaltiriparus minimus</u>)	- -	- -	- -	- -	- -	- -	21 (0)
Wrentit (<u>Chamaea fasciata</u>)	- -	- -	- -	- -	- -	- -	24 (14)
White-breasted Nuthatch (<u>Sitta carolinensis</u>)	- -	18 (0)	- -	- -	23 (0)	56 (0)	- -
Red-breasted Nuthatch (<u>Sitta canadensis</u>)	17 (0)	68 (0)	45 (0)	33 (0)	41 (0)	81 (0)	72 (10)
Brown-headed Nuthatch (<u>Sitta pusilla</u>)	- -	- -	36 (0)	- -	- -	- -	- -
Pygmy Nuthatch (<u>Sitta pygmaea</u>)	- -	- -	- -	- -	18 (0)	19 (0)	24 (0)
Brown Creeper (<u>Certhia familiaris</u>)	33 (0)	45 (0)	27 (0)	27 (0)	27 (9)	94 (0)	72 (21)
House Wren (<u>Troglodytes aedon</u>)	- -	- -	- -	- -	41 (9)	19 (0)	7 (0)

Species		Coniferous Forest Region						
		Northeast Immature	Northeast Mature	Southeast	Northern	Rocky Mountain	Sierra Nevada	Northwest Coastal
Sample Size:		12	22	11	15	22	16	29
Winter Wren (<u>Troglodytes troglodytes</u>)		17 (0)	45 (0)	45 (0)	53 (0)	- (-)	38 (0)	69 (0)
Bewick's Wren (<u>Thryomanes bewickii</u>)		- (-)	- (-)	- (-)	- (-)	- (-)	- (-)	17 (0)
Carolina Wren (<u>Thryothorus ludovicianus</u>)		- (-)	- (-)	27 (0)	- (-)	- (-)	- (-)	- (-)
Catbird (<u>Dumetella carolinensis</u>)		- (-)	5 (0)	9 (0)	- (-)	- (-)	- (-)	- (-)
Brown Thrasher (<u>Toxostoma rufum</u>)		- (-)	5 (0)	18 (0)	- (-)	- (-)	- (-)	- (-)
American Robin (<u>Turdus migratorius</u>)		17 (0)	73 (5)	45 (0)	53 (0)	68 (5)	94 (6)	38 (0)
Varied Thrush (<u>Ixoreus naevius</u>)		- (-)	- (-)	- (-)	13 (0)	5 (0)	- (-)	17 (0)
Townsend's Solitaire (<u>Myadestes townsendi</u>)		- (-)	- (-)	- (-)	- (-)	27 (0)	94 (0)	3 (0)
Wood Thrush (<u>Hylocichla mustelina</u>)		- (-)	41 (5)	82 (45)	- (-)	- (-)	- (-)	- (-)
Hermit Thrush (<u>Hylocichla guttata</u>)		75 (33)	45 (0)	9 (0)	27 (0)	41 (5)	75 (0)	38 (3)
Swainson's Thrush (<u>Hylocichla minima</u>)		- (-)	45 (0)	36 (0)	100 (20)	18 (0)	- (-)	31 (0)
Gray-checked Thrush (<u>Hylocichla minima</u>)		- (-)	- (-)	- (-)	13 (0)	- (-)	- (-)	- (-)
Veery (<u>Hylocichla fuscescens</u>)		- (-)	36 (0)	27 (0)	- (-)	- (-)	- (-)	- (-)
Eastern Bluebird (<u>Sialia sialis</u>)		- (-)	- (-)	27 (0)	- (-)	- (-)	- (-)	- (-)
Western Bluebird (<u>Sialia mexicana</u>)		- (-)	- (-)	- (-)	- (-)	23 (23)	- (-)	3 (0)
Mountain Bluebird (<u>Sialia currucoides</u>)		- (-)	- (-)	- (-)	- (-)	9 (0)	19 (19)	- (-)
Blue-gray Gnatcatcher (<u>Polioptila caerulea</u>)		- (-)	- (-)	27 (0)	- (-)	- (-)	- (-)	- (-)
Golden-crowned Kinglet (<u>Regulus satrapa</u>)		50 (8)	45 (5)	45 (27)	40 (0)	27 (0)	81 (25)	66 (21)
Ruby-crowned Kinglet (<u>Regulus calendula</u>)		75 (25)	41 (0)	- (-)	60 (0)	64 (18)	6 (0)	7 (0)

		Coniferous Forest Region						
Species	Sample Size:	Northeast Immature	Northeast Mature	Southeast	Northern	Rocky Mountain	Sierra Nevada	Northwest Coastal
		12	22	11	15	22	16	29
Cedar Waxwing (<i>Bombycilla cedrorum</i>)		- -	18 (0)	- -	13 (0)	- -	- -	- -
Starling (<i>Sturnus vulgaris</i>)		- -	5 (0)	- -	- -	- -	- -	3 (0)
Solitary Vireo (<i>Vireo solitarius</i>)		8 (0)	36 (0)	36 (0)	- -	27 (0)	56 (0)	- -
White-eyed Vireo (<i>Vireo griseus</i>)		- -	- -	27 (0)	- -	- -	- -	- -
Hutton's Vireo (<i>Vireo huttoni</i>)		- -	- -	- -	- -	- -	- -	24 (0)
Yellow-throated Vireo (<i>Vireo flavifrons</i>)		- -	- -	9 (0)	- -	- -	- -	- -
Red-eyed Vireo (<i>Vireo olivaceus</i>)		8 (0)	73 (0)	64 (0)	47 (0)	- -	- -	- -
Philadelphia Vireo (<i>Vireo philadelphicus</i>)		- -	5 (0)	- -	- -	- -	- -	- -
Warbling Vireo (<i>Vireo gilvus</i>)		- -	- -	- -	- -	32 (0)	38 (0)	10 (0)
Black-and-White Warbler (<i>Mniotilta varia</i>)		- -	64 (0)	- -	40 (0)	- -	- -	- -
Tennessee Warbler (<i>Vermivora peregrina</i>)		8 (8)	27 (5)	- -	27 (7)	- -	- -	7 (0)
Orange-crowned Warbler (<i>Vermivora celata</i>)		- -	- -	- -	13 (0)	- -	- -	24 (0)
Nashville Warbler (<i>Vermivora ruficapilla</i>)		58 (8)	45 (0)	- -	33 (0)	- -	69 (0)	- -
Virginia's Warbler (<i>Vermivora virginiae</i>)		- -	- -	- -	- -	14 (0)	- -	- -
Parula Warbler (<i>Parula americana</i>)		- -	27 (0)	- -	7 (0)	- -	- -	- -
Yellow Warbler (<i>Dendroica petechia</i>)		- -	5 (5)	- -	7 (0)	5 (0)	- -	3 (0)
Magnolia Warbler (<i>Dendroica magnolia</i>)		50 (0)	55 (32)	36 (27)	47 (13)	- -	- -	3 (0)
Cape May Warbler (<i>Dendroica tigrina</i>)		- -	18 (10)	- -	7 (0)	- -	- -	- -
Yellow-rumped Warbler (<i>Dendroica coronata</i>)		100 (8)	59 (0)	- -	73 (13)	77 (14)	63 (6)	3 (0)

Coniferous Forest Region

Species	Sample Size:	Northeast Immature	Northeast Mature	Southeast	Northern	Rocky Mountain	Sierra Nevada	Northwest Coastal
		12	22	11	15	22	16	29
Townsend's Warbler (<i>Dendroica townsendi</i>)		-	-	-	13 (7)	-	-	7 (0)
Black-throated Green Warbler (<i>Dendroica virens</i>)	42 (0)		64 (27)	27 (0)	27 (0)	-	-	-
Hermit Warbler (<i>Dendroica occidentalis</i>)	-	-	-	-	-	-	38 (0)	34 (7)
Black-throated Blue Warbler (<i>Dendroica caerulescens</i>)	8 (0)		14 (0)	18 (0)	-	-	-	-
Blackburnian Warbler (<i>Dendroica fusca</i>)	8 (0)		91 (23)	36 (9)	-	-	-	-
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	-		23 (5)	-	40 (0)	-	-	-
Bay-breasted Warbler (<i>Dendroica castanea</i>)	33 (17)		32 (18)	-	20 (7)	-	-	3 (0)
Blackpoll Warbler (<i>Dendroica striata</i>)	-		5 (0)	-	7 (0)	-	-	3 (3)
Pine Warbler (<i>Dendroica pinus</i>)	-		14 (9)	45 (18)	-	-	-	-
Prairie Warbler (<i>Dendroica discolor</i>)	-		-	45 (0)	-	-	-	-
Yellow-throated Warbler (<i>Dendroica dominica</i>)	-		-	9 (0)	-	-	-	-
Palm Warbler (<i>Dendroica palmarum</i>)	8 (0)		-	-	20 (7)	-	-	-
Ovenbird (<i>Seiurus aurocapillus</i>)	25 (17)		86 (27)	55 (18)	40 (27)	-	-	-
Northern Waterthrush (<i>Seiurus noveboracensis</i>)	-		23 (0)	18 (0)	-	-	-	3 (0)
Yellowthroat (<i>Geothlypis trichas</i>)	17 (0)		36 (5)	-	-	-	5 (0)	-
Yellow-breasted Chat (<i>Icteria virens</i>)	-		-	9 (0)	-	-	-	-
MacGillivray's Warbler (<i>Oporornis tolmiei</i>)	-		-	-	-	5 (5)	-	14 (0)
Mourning Warbler (<i>Oporornis philadelphia</i>)	-		14 (0)	-	40 (0)	-	-	-
Hooded Warbler (<i>Wilsonia citrina</i>)	-		-	36 (9)	-	-	-	-

Coniferous Forest Region

Species	Coniferous Forest Region						
	Northeast Immature	Northeast Mature	Southeast	Northern	Rocky Mountain	Sierra Nevada	Northwest Coastal
Sample Size:	12	22	11	15	22	16	29
Wilson's Warbler (<u>Wilsonia pusilla</u>)	8 (0)	- -	- -	7 (0)	5 (0)	- -	45 (24)
Canada Warbler (<u>Wilsonia canadensis</u>)	- -	68 (9)	18 (0)	27 (20)	- -	- -	- -
American Redstart (<u>Setophaga ruticilla</u>)	8 (0)	23 (0)	- -	- -	- -	- -	3 (3)
Rusty Blackbird (<u>Euphagus carolinus</u>)	- -	5 (0)	- -	7 (0)	- -	- -	- -
Red-winged Blackbird (<u>Agelaius phoeniceus</u>)	- -	5 (0)	- -	- -	- -	- -	- -
Common Grackle (<u>Quiscalus quiscula</u>)	- -	14 (0)	27 (0)	- -	- -	- -	- -
Brown-headed Cowbird (<u>Molothrus ater</u>)	- -	36 (0)	55 (0)	- -	- -	- -	- -
Baltimore Oriole (<u>Icterus galbula</u>)	- -	5 (0)	- -	- -	- -	- -	- -
Western Tanager (<u>Piranga ludoviciana</u>)	- -	- -	- -	- -	41 (9)	94 (0)	38 (0)
Scarlet Tanager (<u>Piranga olivacea</u>)	- -	45 (0)	55 (0)	7 (0)	- -	- -	- -
Summer Tanager (<u>Piranga rubra</u>)	- -	- -	36 (0)	- -	- -	- -	- -
Cardinal (<u>Richmondia cardinalis</u>)	- -	5 (0)	55 (9)	- -	- -	- -	- -
Rose-breasted Grosbeak (<u>Pheucticus ludovicianus</u>)	- -	18 (0)	- -	7 (0)	- -	- -	- -
Black-headed Grosbeak (<u>Pheucticus melanocephalus</u>)	- -	- -	- -	- -	18 (0)	38 (13)	14 (0)
Evening Grosbeak (<u>Hesperiphona vespertina</u>)	- -	- -	- -	- -	9 (0)	44 (0)	10 (0)
Indigo Bunting (<u>Passerina cyanea</u>)	- -	5 (0)	36 (0)	- -	- -	- -	- -
Lazuli Bunting (<u>Passerina amoena</u>)	- -	- -	- -	- -	5 (0)	13 (0)	- -
Purple Finch (<u>Carpodacus purpureus</u>)	25 (0)	73 (0)	27 (0)	40 (0)	- -	25 (0)	21 (0)
Cassin's Finch (<u>Carpodacus cassinii</u>)	- -	- -	- -	- -	27 (0)	69 (0)	- -

Species	Sample Size:	Coniferous Forest Region						
		Northeast Immature	Northeast Mature	Southeast	Northern	Rocky Mountain	Sierra Nevada	Northwest Coastal
		12	22	11	15	22	16	29
House Finch (<u>Carpodacus mexicanus</u>)		- -	- -	- -	- -	9 (0)	- -	3 (0)
Pine Grosbeak (<u>Pinicola enucleator</u>)		- -	5 (0)	- -	- -	18 (0)	- -	3 (0)
Common Redpoll (<u>Acanthis flammea</u>)		- -	- -	- -	13 (7)	- -	- -	- -
Pine Siskin (<u>Spinus pinus</u>)		8 (0)	- -	9 (0)	13 (0)	64 (9)	13 (0)	38 (3)
American Goldfinch (<u>Spinus tristis</u>)		- -	14 (0)	- -	- -	- -	- -	14 (0)
Lesser Goldfinch (<u>Spinus psaltria</u>)		- -	- -	- -	- -	18 (0)	- -	- -
Red Crossbill (<u>Loxia curvirostra</u>)		- -	- -	9 (0)	- -	14 (0)	- -	- -
White-winged Crossbill (<u>Loxia leucoptera</u>)		- -	- -	- -	20 (0)	- -	- -	3 (0)
Green-tailed Towhee (<u>Chlorura chlorura</u>)		- -	- -	- -	- -	14 (0)	13 (0)	- -
Rufous-sided Towhee (<u>Pipilo erythrophthalmus</u>)		- -	32 (0)	63 (9)	- -	18 (0)	25 (0)	34 (0)
Savannah Sparrow (<u>Passerculus sandwichensis</u>)		- -	- -	- -	7 (0)	- -	- -	- -
Junco (<u>Junco hyemalis</u>)		100 (42)	55 (5)	45 (27)	53 (27)	41 (27)	100 (94)	97 (24)
Gray-headed Junco (<u>Junco caniceps</u>)		- -	- -	- -	- -	36 (14)	- -	- -
Chipping Sparrow (<u>Spizella passerina</u>)		8 (0)	23 (5)	18 (0)	40 (27)	55 (14)	25 (0)	14 (0)
Brewer's Sparrow (<u>Spizella breweri</u>)		- -	- -	- -	- -	5 (0)	19 (0)	- -
Field Sparrow (<u>Spizella pusilla</u>)		- -	5 (0)	18 (0)	- -	- -	- -	- -
White-crowned Sparrow (<u>Zonotrichia leucophrys</u>)		- -	- -	- -	7 (0)	5 (5)	- -	14 (0)
White-throated Sparrow (<u>Zonotrichia albicollis</u>)		100 (25)	55 (9)	- -	53 (20)	- -	- -	- -
Fox Sparrow (<u>Passerella iliaca</u>)		- -	- -	- -	7 (0)	5 (0)	44 (0)	3 (0)

		Coniferous Forest Region						
		Northeast Immature	Northeast Mature	Southeast	Northern	Rocky Mountain	Sierra Nevada	Northwest Coastal
Species	Sample Size:	12	22	11	15	22	16	29
<hr/>								
Lincoln's Sparrow (<i>Melospiza lincolnii</i>)	8 (0)	- (0)	- (0)	- (0)	13 (0)	5 (0)	- (0)	3 (0)
Song Sparrow (<i>Melospiza melodia</i>)	- (0)	14 (0)	- (0)	7 (0)	- (0)	- (0)	- (0)	24 (0)
Swamp Sparrow (<i>Melospiza georgiana</i>)	- (0)	- (0)	9 (0)	- (0)	- (0)	- (0)	- (0)	- (0)
<hr/>								
Number of Species Recorded		39	76	59	59	61	45	71
Number of Dominant Species		11	17	10	12	17	9	15

California. A much smaller set of species dominates the avifauna in each of these regions. Over the range of coniferous forest situations, 9-17 species were numerically most abundant in the collection of breeding censuses from any single region. Thus only 17-28 percent of the species present in a region normally attain dominant status (i.e. are the most abundant species recorded in at least one census). Many of the species listed in table 1 occur in only one or two of the seven arbitrarily-defined regional types. Roughly 15 percent of the 148 species recorded are relatively wide-spread, occurring in at least five of the seven types. Northern three-toed Woodpeckers, Gray Jays, Swainson's Thrush, Solitary Vireo, Magnolia Warblers and Rufous-sided Towhees were recorded in censuses in five different regional types, while Pileated Woodpecker, Yellow-bellied Sapsuckers, Hairy Woodpeckers, Black-capped Chickadees, Winter Wrens, Ruby-crowned Kinglets, Yellow-rumped Warblers, Purple Finches and Pine Siskins were recorded in six regional types. Eight species (Common Flicker, Red-Breasted Nuthatch, Brown Creeper, American Robin, Hermit Thrush, Golden-Crowned Kinglet, Junco and Chipping Sparrow) were present in censuses in all regions of coniferous forests in North America and can thus be considered to be the most representative species group in this vegetation type over North America as a whole. Relatively few of the species attaining dominance (greatest abundance) in censuses were wide-spread. Golden-crowned Kinglets attained a dominant status in censuses in at least five of the seven regions, while Juncos were dominant in at least some censuses in all areas of North American coniferous forests. Much more could be said of these patterns of species distribu-

tions, but the patterns in table 1 are apparent: coniferous forest avifaunas contain a large variety of bird species over North America as a whole, and various regions of coniferous forests contain relatively rich avifaunas. While some species are distinctive to each of the regions or habitats, others achieve a very broad distribution, and it is frequently these broadly-distributed forms which also attain numerical dominance in census plots. We may offer the speculation that among birds the species dominating local communities in many habitat types may frequently be those with the broadest or at least broad geographical distributions. This is a speculation of considerable interest in terms of management of nongame bird populations, and should be explored more rigorously.

Community Structure

Superimposed upon these patterns of species distributions are the patterns of breeding species assemblages or "communities" which are portrayed in breeding censuses. The term "community" in this context refers only to the assemblage of species which is encountered in an area-defined census and does not carry implicit assumptions of any degree of integration or coevolution of these community components. Since these "communities" are defined by the breeding censuses they are sensitive to the area which is included within a given census. I have not included censuses conducted in very small sample plots or in extremely large and heterogeneous areas, and therefore believe that whatever bias introduced by area effects is consistent throughout the censuses upon which

this analyses is based.

Avian communities are characterized by a variety of features: breeding densities, standing crop biomass, numbers of breeding species, the degree of species dominance and various facets of the ecological structuring of the avifauna. Calculated values for species numbers, densities, biomass, and species dominance for censuses conducted in the locations indicated in figure 1 are detailed in Appendix I, along with the appropriate reference citations. Table 2 summarizes the results of these censuses in relation to the various coniferous forest regions outlined in figure 1.

Species Numbers

A quick scanning of the values in Appendix I reveals that there is substantial variation in the number of species characteristically breeding in coniferous forest habitat. Species numbers ranged from 6 to 32 in the sampling of censuses included in this analysis, although the maximum values could be increased substantially by inclusion of censuses taken in heterogeneous habitat types (e.g., mixed coniferous-deciduous woodlands). The mean number of breeding species also varies between the different regions of coniferous forest habitat. Mature Northeastern forests, Southeastern pine forests and forests in the Sierra Nevadas of California all support relatively large numbers of breeding species, while the other regions appear to contain consistently fewer species. By way of comparison these species numbers are roughly 2-4 times those recorded in comparable breeding censuses in rangeland or shrubsteppe habitats in North America (Wiens and Dyer, this symposium).

Total Density

Coniferous forests characteristically support large numbers of individuals of the breeding species present. Breeding densities (numbers of individuals per square kilometer, as calculated from the census results) ranged from under 200 to over 2,500 among the range of censuses surveyed. Average densities were high in Northeastern mature coniferous forests, Southeastern forests and Northwest Coastal Forests, intermediate in Sierra Nevada and Rocky Mountain forests, and relatively low in Northern boreal forests and immature stages of Northeastern forests. There is considerable variation in plot densities within each of these regions, however, which obscures the significance of these differences in mean densities.

Total Biomass

Values for the breeding density of each species may be multiplied by the average body weight (grams wet wt) of that species to determine the standing biomass of a species present in a census area. Total "community" standing crop biomass values (expressed as grams per hectare) ranged from around 20 to over 600 over the entire range of plots censused. Average standing crop biomass was highest in Northwest Coastal, Southeastern, and mature Northeastern coniferous forests, somewhat lower in Sierra Nevada and Rocky Mountain forests, and low in Northern and immature Northeastern coniferous stands. As with density, there is considerable plot variation in biomass values, which to a large degree results from the variation in the density values themselves.

There is, of course, a close relation between total density and standing crop biomass in a stand, since one is derived by calculation from the other. The nature of this relationship, however, differs in different sorts of coniferous forests (figure 2). In all forest types, biomass increases with increasing density, but the increase occurs at different rates.

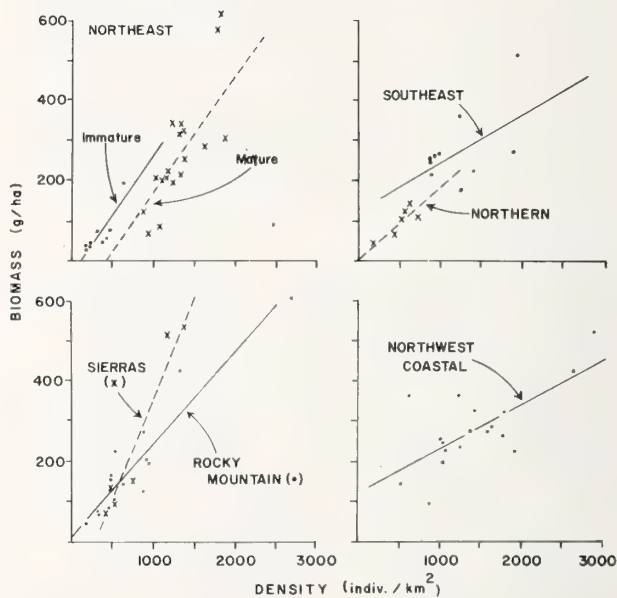


Figure 2.--Relations between breeding density and standing crop biomass in avifaunas of coniferous forest regions in North America. Census values are detailed in Appendix I; lines are least squares regressions, and are intended for general comparisons only.

Table 2.--Features of breeding bird communities in coniferous forests of different regions of North America, generalized from the census values given in Appendix I. Values are means, with standard deviations in parentheses.

Region	Sample Size	Number of Species	Density	Standing Crop Biomass	Dominance	
			Indiv./km ²	g/ha	1 species	2 species
Northeast (Immature)	9	11.1 (3.7)	328.5 (150.2)	65.3 (50.3)	27 (8.7)	46 (9.8)
Northeast (Mature)	18	22.6 (4.2)	1340.6 (343.0)	272.9 (145.5)	19 (7.3)	30 (9.1)
Southeast	10	21.6 (5.5)	1220.6 (406.5)	281.4 (94.81)	21 (6.6)	35 (10.7)
Northern	4	14.5 (3.9)	465.8 (215.6)	80.3 (32.0)	22 (6.1)	39 (7.1)
Rocky Mountain	17	14.0 (5.0)	735.8 (575.3)	188.0 (146.6)	25 (9.2)	41 (12.1)
Sierra Nevada	6	21.3 (5.0)	796.3 (410.8)	250.6 (215.1)	17 (3.4)	31 (6.6)
Northwest Coastal	17	15.4 (6.1)	1456.1 (621.4)	283.1 (102.3)	23 (8.5)	37 (10.3)

The rate of increase is most rapid in Northeastern coniferous forests and Sierra Nevada avifaunas and markedly less precipitous in Northwestern, Northern and Southeastern coniferous forests. What this says, of course, is that the increases in density in these latter regions are through addition of relatively small-sized individuals to the avifauna, while comparable incremental increases in density in Northeastern and Sierra Nevada forests involve the addition of individuals of larger mean body size. In Northeastern coniferous forests, immature stands supporting the same number of individuals as a comparable mature forest stand contain more biomass (i.e. the mean size of individual birds is greater). These patterns suggest that there may be some rather basic differences in the allocation of individual birds to body size classes among different regions in coniferous forests, perhaps similar to those apparent in rangeland avifaunas (Wiens and Dyer this symposium) or documented in Southeastern forests by McNaughton and Wolf (1972). Satisfactory explanation of these differences in density-biomass relations must be tied to patterns of resource allocation among different sized species with different energetic strategies. A more detailed examination of these patterns is now underway (Wiens, unpublished).

There are fundamental differences in the relations between total density and total biomass in coniferous forest environments and in rangeland habitats. Standing crop biomass in rangeland frequently approaches that found in coniferous forests stands, while density rarely if ever does so. Averaging over all habitat types or regions, standing crop biomass in coniferous forests is roughly twice that in rangeland and shrubsteppe habitat, while total breeding density is nearly 3.5 times as great in coniferous habitats. This, of course, reflects the greater degree of dominance by large-sized species in rangeland habitats. In a set of six coniferous forest stands in western Oregon (Wiens and Nussbaum 1975), 0-9 percent of the individuals present were "large" (greater than 80 grams body weight) and 55-83 percent of the individuals were "tiny" (10 grams or less). In various rangeland habitat types, on the other hand, 11-36 percent of the individuals present were large, and individuals in the "tiny" size class were entirely absent (Wiens and Dyer this symposium). These differences are of course related in a general way to opportunities for resource utilization in the different habitat types. For example, body size may be constrained to some degree by the nature of the substrate used during foraging. In most rangeland environments foraging is conducted while standing on

the ground, which of course will support individuals of substantial weight. In coniferous forests, on the other hand, many foraging opportunities are in the outer zones of canopies, where the twigs or needles will support only small individuals or where food resources may be available only to individuals of relatively small dimensions.

Species Dominance

Given the apparent richness in species numbers and densities in most coniferous forest types, one should expect that generally no single species should markedly dominate the avifauna (i.e. account for most of the individuals present in the stand). I have calculated species dominance rather simply, as the percent of all individuals recorded which belong to the single most abundant species, and to the combined populations of the two most abundant species in the census. The census summaries of table 2 suggest that on the average 17-27 percent of the individuals present belong to the single most abundant species while 30-46 percent of the individuals are included in the two most abundant species. Dominance tends to be relatively high in immature stages of Northeastern coniferous forests and in Rocky

Mountain forests, and relatively low in mature Northeastern forests and Sierra Nevada forests. The difference between Sierra Nevada and Rocky Mountain avifaunas is interesting and reflects the fact that while densities are similar in the two forest regions, Sierra avifaunas on the average contain 7 more species per census plot than Rocky Mountain areas. Dominance of the single most abundant species is related to species number for coniferous forests in all regions in figure 3. As expected, there is a general tendency for dominance to decrease as species numbers increase, but in none of the types does dominance closely approach the minimum dominance possible (i.e. when all species present are equally abundant). Thus coniferous forest avifaunas, unlike those of rangeland habitats, are not strongly dominated by one or two species. The species which contribute to these dominance values for the coniferous forest censuses are indicated in table 1.

Non-North American Coniferous Forests Censuses

We may briefly compare these results of censuses in North American coniferous forests with similar counts conducted in a sampling of coniferous forests stands elsewhere in the world (table 3). This list includes a much more

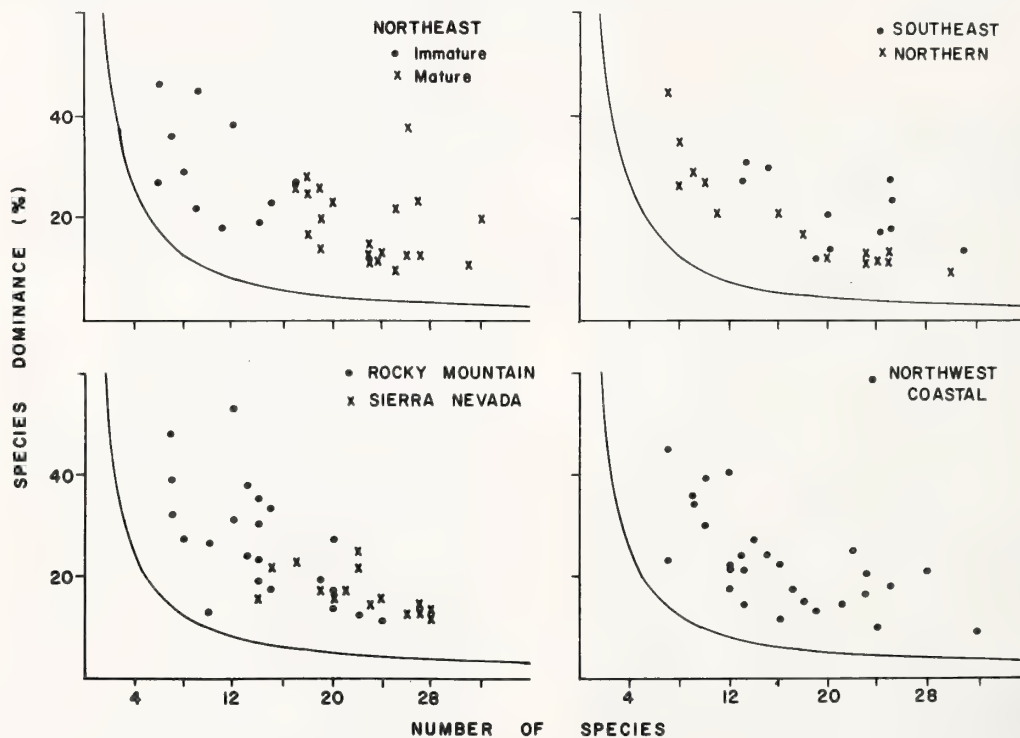


Figure 3.-- Relationship between number of breeding species and single species dominance (the proportion of all individuals recorded belonging to the single most abundant species) in North American coniferous forests. The curve indicates the minimum dominance possible, when all species present are equally abundant (and diversity is therefore maximum).

Table 3.--Avian community attributes in a sampling of non-North American breeding censuses of coniferous forests. Many of these censuses were conducted in heterogeneous habitats, and thus are not directly comparable with the results of the North American censuses.

Area	Forest Type	No. Samples	No. Species	Density (indiv/km ²)	Dominance		Reference
					1 Species	2 Species	
Czechoslovakia	<u>Picea abies</u>	1	49	1273.0	-	-	Turcek 1956
Poland	<u>Pinus-Calluna</u>	5	14.6	864.0	17	29	Jabłonski 1967
	<u>Pinus-Vaccinium</u>	5	13.6	3013.2	15	28	"
	"	5	13.2	2864.8	18	31	"
	<u>Pinus-Quercus</u>	5	18.4	7629.2	13	23	"
Norway	<u>Picea</u> (homogeneous ²)		8.5	1450.5	29	46	Fremming & Slagsvold 1966,1967
	<u>Picea</u> (mixed)	2	8.5	1275.0	28	48	"
Sweden	<u>Picea</u>	1	10	342.9	22	33	Enemar et al 1965
Finland	Open <u>Picea</u>	4	22.3	595.4	21	37	Haapanen 1965
	Brushy <u>Picea</u>	4	13.2	410.5	21	36	"
	Open <u>Picea-Pinus</u>	3	15.3	594.0	23	36	"
	Open <u>Pinus</u>	4	17.3	265.9	20	34	"
	Brushy <u>Pinus</u>	3	10.0	230.6	26	47	"
New Zealand	<u>Pinus nigra</u>	1	12	607.9	26	46	Gibb 1961
	<u>Pinus radiata</u>	1	12	1203.4	29	55	"
	<u>Pinus ponderosa</u>	1	12	822.8	37	54	"
	<u>Pseudotsuga taxifolia</u>	4	8	523.9	30	59	"

heterogeneous assemblage of census types than those comprising the North American data. Many of the forest stands are managed plantations or mixed coniferous-deciduous shrub woodlands and therefore the calculations serve only to provide a general comparison with North American types. In general, the number of breeding species present appears to be similar to that of North American coniferous forests. Species numbers were low in the Norwegian and Swedish forests, perhaps because these are northern areas and because the census plots were small. Species numbers are also low in the New Zealand forests studied by Gibb (1961), but there all four forest types are dominated by introduced tree species and the rapidity and extent of

their colonization by even this many native bird species is remarkable. Estimates of breeding densities are much more variable, perhaps reflecting errors introduced through the inclusion of censuses made employing vastly different techniques. The Polish census results of Jabłonski (1967) seem especially high, while those of Haapanen (1965) in Finland seem rather low. In any case, over the entire range of values there is general agreement with the overall mean density of the North American coniferous forest habitat. Unfortunately, information on body weights of many European species was not readily available to me so no biomass calculations have been made. Species dominance in these forests seems generally

similar to that in the North American forests. Certainly the data do not suggest that North American coniferous forests deviate in any marked fashion from their coniferous forest counterparts elsewhere in the world.

Ecological Structure of the Avifauna

These analyses of density, biomass, and dominance are based upon species as the chief categories, but documentations based upon ecological and behavioral categories may be equally meaningful. The impetus for such an approach comes from many fine studies of the behavioral ecology of coniferous forest species or species assemblages (e.g., Balda 1969, Salt 1957, Anderson 1970, MacArthur 1958, Sturman 1968a, 1968b, Stallcup 1968, Jackson 1970, Tate 1973, Winternitz 1973) which have documented the patterns of habitat utilization during the breeding or nonbreeding seasons. It is upon such information that habitat management strategies of single species or species groups should ideally be based, for it documents the importance of specific habitat features to the birds (for example, the importance of dead snags for many woodpecker species, Jackman 1975). The results of these studies pertain to too small a group of species and are too detailed to summarize here. However, they do provide a basis for classifying the various species recorded in coniferous forest breeding censuses (table 1) into several very general ecological categories. These categories, which follow those originally defined by Salt (1957), and modified by Bock and Lynch (1970) and Anderson (1970, 1972), group species according to the substrate type in which foraging occurs (foliage, timber, ground, and air) and the major component of the diet during the breeding season (invertebrates or seeds). The timber-feeding category (most of which are largely insectivorous) is further divided into forms which practice searching tactics and those which drill timber to obtain food. After each species recorded in a census has been categorized in this manner, density and biomass values may be totaled for each category to provide information on the structuring of the avifaunas according to these ecologically-defined units. The results of these analyses are summarized for the various coniferous forest regions in table 4 and figure 4.

It is apparent from this analysis (figure 4) that foliage-feeding forms numerically dominate the avifauna in all North American coniferous forests, with ground-feeding, timber-foraging and aerial feeders less important, in decreasing order. The proportional dominance of foliage-feeders is greatest in northeastern mature and southeastern coniferous forests. All ground-foragers attain their greatest

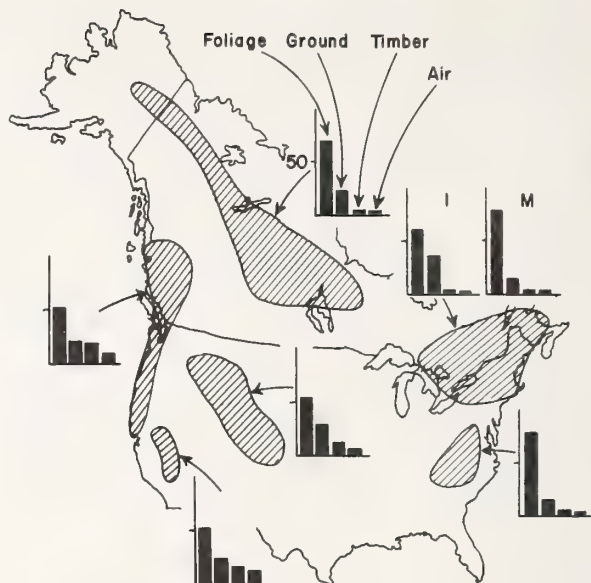


Figure 4.--Relative densities (percentages of total density) of major ecological "guilds" of breeding birds in coniferous forest regions of North America. Values are means of the censuses listed for each area in Appendix I. For the Northwest region, I = Immature forest stages, M = Mature forest stages.

"importance" in early successional stages of northeastern forests, and timber and air-feeding forms appear to be numerically most abundant in western coniferous forests. When the foliage-feeding "guild" (Root 1967) is divided according to diet habits (table 4) we see that insectivorous forms contribute the greatest share of the foliage-feeding element in all forest types, while the percent of all individuals foraging for seeds or fruits in canopy foliage is relatively uniform in all forests except those of southeastern United States. Seed-eaters predominate in the ground-foraging component, especially in immature northeastern forests. Among the timber-foraging group "searchers" appear to be more prevalent in western montane and northwest coastal coniferous forests than in the remainder of North America, and drilling forms show a similar tendency to increase in relative density as one moves west.

Because of its importance in coniferous forests throughout North America it is instructive to consider the foliage-feeding element in more detail. Table 1 suggests that various warbler species are important constituents of coniferous forests in many areas, and since these are all insectivorous foliage-feeding species we may consider their contribution to

Table 4.--Percentages of total breeding density (D) and biomass (B) in major ecological categories or "guilds" of coniferous forest birds, averaged by forest regions. Standard deviations are given in parentheses; N = sample size.

Region	N	Foliage-feeding				Ground-feeding				Timber-feeding				Air-feeding				Miscellaneous			
		Insect		Seed		Insect		Seed		Searching		Drilling		D		B		D		B	
		D	B	D	B	D	B	D	B	D	B	D	B	D	B	D	B	D	B	D	B
Northeast Immature	7	49 (16.2)	29 (15.1)	11 (7.9)	18 (11.2)	2 (2.1)	5 (8.6)	33 (12.3)	40 (13.6)	3 (4.0)	2 (2.5)	1 (1.6)	4 (7.4)	2 (1.6)	1 (1.1)	-	-	-	-	-	-
Northeast Mature	17	61 (11.1)	36 (12.3)	15 (12.2)	27 (20.4)	5 (3.2)	15 (10.1)	10 (5.7)	11 (7.1)	3 (2.8)	2 (1.0)	2 (2.8)	7 (8.2)	4 (3.6)	4 (4.8)	-	-	-	-	-	-
Southeast	11	47 (8.2)	24 (10.5)	29 (16.2)	50 (21.1)	5 (6.5)	7 (11.1)	10 (13.2)	9 (11.1)	3 (3.5)	2 (2.2)	2 (2.7)	8 (8.8)	3 (3.2)	2 (2.4)	-	-	-	-	-	-
Northern	6	55 (6.8)	33 (9.3)	14 (9.0)	27 (16.5)	5 (3.1)	7 (5.9)	17 (11.4)	16 (10.3)	2 (1.9)	1 (0.8)	3 (4.9)	13 (20.1)	5 (5.4)	2 (2.2)	-	-	-	-	-	-
Rocky Mountain	22	36 (13.7)	23 (14.4)	17 (11.1)	28 (18.3)	8 (5.6)	14 (11.4)	20 (13.2)	16 (11.8)	8 (6.6)	3 (2.9)	3 (3.6)	10 (13.5)	6 (6.3)	4 (5.7)	1 (1.8)	t	-	-	-	-
Sierra Nevada	12	34 (11.7)	21 (10.6)	17 (7.8)	31 (14.6)	6 (4.6)	13 (8.5)	18 (5.0)	13 (6.7)	8 (3.1)	3 (1.9)	5 (2.3)	13 (7.4)	11 (3.6)	5 (1.6)	t	-	-	-	-	-
Northwest Coastal	29	39 (13.2)	22 (10.6)	12 (8.0)	27 (13.2)	5 (4.5)	6 (6.9)	15 (11.1)	14 (7.8)	12 (9.5)	6 (6.1)	6 (8.2)	17 (17.8)	9 (6.2)	6 (5.7)	1 (1.8)	t	-	-	-	-



Figure 5.--Relative densities (percentages of total number of individuals of all species) of warblers (Parulidae) recorded in North American breeding censuses.

the total avian breeding density of various sites as separate component of the foliage-feeding guild. In figure 5 I have plotted several categories of relative densities (i.e., the percentage of all individuals recorded in breeding censuses) of all warbler species combined. It is apparent that warblers constitute the major component of breeding avifaunas throughout northeastern and southeastern United States (especially in mature coniferous forests) while their relative densities are lower in northern boreal forests and lower still in the coniferous forests of the Rocky Mountains, Sierra Nevadas and Northwestern coastal areas. Thus both the number of warbler species (table 1) and their relative and absolute densities are substantially lower in western forests than in eastern North America, and the relative paucity of warblers in the west is not compensated for by a proportionate increase in other foliage-feeding insectivores in these western forests. The relatively low number of warbler species in the west may stem from biogeographic events and speciation processes (Mengel 1964, 1970), but the differences in total densities and biomass of foliage insectivores, especially warblers, immediately suggests that there may be differences in prey resource availability in the different forest regions. The avian data thus suggest that endemic levels of foliage-feeding insects during the breeding season might be expected to be lower in western than eastern coniferous forests and/or perhaps that

population outbreaks or epidemics of defoliating insects might be less frequent and reach less spectacular levels in western than eastern North America. Coniferous forests in the north and northeast more frequently approach true climax conditions than do western forests, and this may influence insect abundance (although not always in certain directions). These regional differences are intriguing, not only for their theoretical significance but for their importance in the formulation of habitat management strategies, and bear closer examination in light of studies of forest entomologists.

Avifaunal Stability

The patterns of avian community structure summarized above are in a sense static representations, for they do not consider temporal variation in population densities or species compositions. Knowledge of the magnitude of temporal change in avifaunal structure is crucial to the formulation of sound management strategies. Thus management plays which attempt to produce stability in inherently fluctuating populations and communities may be inappropriate. On the other hand, evidence of apparent instability in population and community structure may lead us to suspect that management is required, but before implementing such measures it is necessary to determine whether the fluctuations are natural or result from human alterations of the natural systems. Unfortunately, not a great deal of information is available on the inherent stability of bird populations in coniferous forest habitats. There are, of course, several time scales to change or stability of avifaunal structure. Here I consider some selected examples of the patterns of seasonal change, year-to-year fluctuations, and changes during ecological succession. While these examples are by no means exhaustive, they should give some indication of the relative magnitudes of fluctuations characteristic of various coniferous forests.

Seasonal Changes

Anderson's (1970) studies in the coniferous forests of western Oregon (site 31 of figure 1) provide an example of the sorts of seasonal changes which may characterize coniferous forests. Anderson conducted population censuses in several plots along a successional-elevation gradient at six times during the year (figure 6). While there were differences in the patterns exhibited in the different forest types, the general patterns of change are similar in all stands. Total avian density decreased slightly from winter into early spring

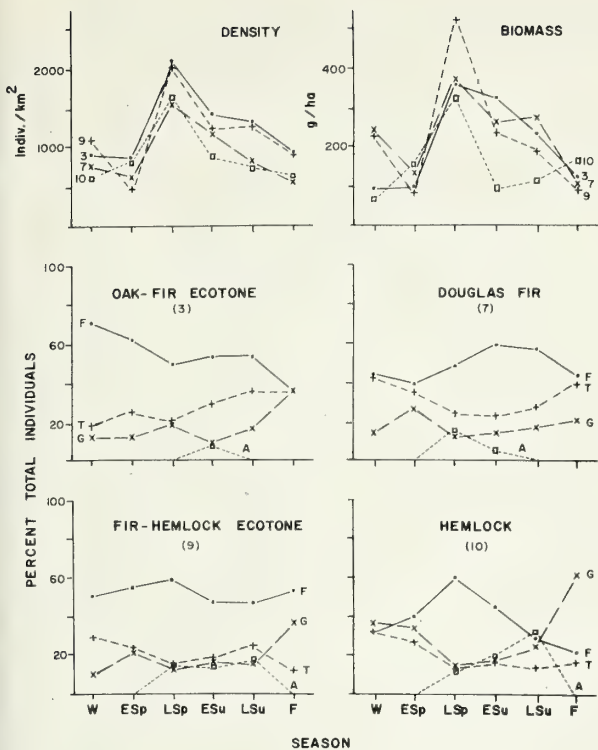


Figure 6.--Seasonal changes in avian density and biomass and in the ecological composition of four stages of coniferous forest succession in western Oregon: 3 = oak-fir ecotone, 7 = douglas fir, 9 = fir-hemlock ecotone, 10 = hemlock "climax". Seasons: W = winter (2 November - 1 March), ES = early spring (2 March - 15 April), LSp = late spring (16 April - 1 June), ESu = early summer (2 June - 15 July), LSu = late summer (16 July - 1 September). F = fall (2 September - 1 November). Ecological categories: F = foliage-feeding, G = ground-foraging, T = timber-foraging, A = air-feeding. From Anderson (1970).

and then more than doubled by the late spring censuses. Peak densities were recorded in all stands at this time, no doubt because of the inclusion of a great many migrant individuals in the censuses. Densities decreased from this late spring peak to the breeding density levels characteristic of early summer, which were higher in all stands than the wintering densities. There was a gradual decline in density from these breeding levels to the wintering levels. Trends in total standing crop biomass were similar, although the magnitude of fluctuation was greater. Total biomass was greatest during the late spring migratory period but in

at least some stands wintering biomass was nearly as great as that recorded during the breeding season. The degree of dominance of the single most abundant species was generally greatest in fall and winter and least during the late spring period.

Anderson's data also permit evaluation of seasonal changes in the ecological structuring of these forest bird communities (figure 6). Here differences between stands are greater but some general trends can nonetheless be distinguished. The occurrence of air-feeding species in the avifauna tended to be restricted to the spring and summer periods in all stands, while ground-feeding forms tended to account for a greater portion of the avifauna in fall than at other times of the year. Foliage- and timber-foraging species assemblages exhibited rather different patterns in the different stands but both underwent seasonal changes in "importance" in most situations.

Annual Changes

Several of the locations indicated in Appendix I have been censused over several successive years and thus provide information on annual changes in density and biomass of the avifauna. To analyze annual variation I calculated the coefficient of variation (CV) of density and biomass values for each census location in which more than one annual breeding census was available. These coefficients of variation were then averaged for each of the major coniferous forest regions of North America and for three European areas (table 5). It appears from this admittedly superficial analysis that total avian densities in northern and northeastern mature forests are extremely stable from year to year, while total densities in immature successional forests in the northeast and in southeastern coniferous forests are notably variable. Annual variability is intermediate in the western forest types. Standing crop biomass variations exhibit the same relative trends, although biomass appears consistently more variable from year to year than density, reflecting shifts in the relative abundances of different-sized species. Densities in the European census areas seem to be about as variable on a year-to-year basis as those in most North American coniferous woodlands.

It is uncertain to what degree these annual variations represent sampling error or true variation in actual densities. Still, the analysis suggests that apart from the apparently stable forests of northern and northeastern North America coniferous forests, avifaunas undergo substantial variations in density and biomass from year to year. In general, these

Table 5.--Coefficients of variation^{1/} of breeding density and biomass values recorded in censuses conducted over several (2-5) successive years in coniferous forest stands.

Region	Sites ^{2/}	Density			Biomass		
		\bar{x}	s	range	\bar{x}	s	range
Northeast Immature	3,8	26.2	6.6	21.6-30.9	30.1	0.9	29.5-30.7
Northeast Mature	14,16,17	2.3	0.4	2.1-2.8	5.7	3.3	1.9-7.8
Southeast	18	37.2	-	-	39.3	-	-
Northern	12(2)	2.2	0.6	1.8-2.6	12.5	4.4	9.4-15.6
Rocky Mountain	38,40,43,47	16.7	12.9	5.4-35.2	31.8	19.9	18.0-54.7
Sierra Nevada	35(2),?,36(2)	17.2	3.0	14.4-21.9	17.9	6.6	10.5-25.2
Northwest Coastal	33(2), 37(2)	11.4	14.1	2.4-32.3	17.2	9.2	12.3-31.0
Poland	-	24.7	3.5	21.4-29.6	-	-	-
Norway	-	19.9	7.3	14.7-25.0	-	-	-
Finland	-	11.5	4.9	5.6-17.1	-	-	-

^{1/} Coefficient of variation = $\frac{100 s}{\bar{x}}$; where entries are yearly values.

^{2/} Numbers refer to codes in Appendix I and Figure 1.

coefficients of variation agree rather closely with those characterizing breeding avifaunas in various rangeland habitat types (Wiens and Dyer, this symposium). Thus the relatively diverse avifaunas of most coniferous forests appear to be no more stable on an annual basis than the low-diversity assemblages characterizing open rangeland habitats.

"Successional" Changes

Coniferous forest avifaunas also undergo change over a longer time interval, as the vegetation changes during ecological succession following disturbances toward the climax condition. The differences between avifaunas of "immature" and mature coniferous forests of the Northeast (table 2) are probably representative of the general trends: early stages support fewer species and individuals and less biomass than mature stages, and the species tend on the average to be larger and ecologically more

dominant. The studies of Anderson (1970, 1972), however, permit closer definition of the changes during succession, at least in the oak-douglas fir-hemlock sequence typical in western Oregon. Here total breeding densities were highest in oak-fir and fir-hemlock ecotonal stands, and lower in "pure" fir or hemlock stands, with the lowest densities recorded in the "climax" hemlock stand (figure 6). Distributions of breeding biomass and species diversity followed similar trends. These results demonstrate the difficulty of making clear assessments of succession-defined changes, for succession inevitably involves transitional stages, and vegetational diversity (in flora and structure) is frequently greater in such transitions, influencing bird populations accordingly. Further, in many areas of western North America, successional sequences are often associated with elevational gradients, so that several interacting sets of factors may contribute to the determination of avian community structure. Thus the censuses from western Oregon summarized by Wiens and Nussbaum (1975) followed

not only a successional series, but were arrayed along moisture and temperature gradients as well (figure 7). In that series of stands, as in Anderson's, greatest avian density and biomass were recorded in "transitional" stands (see Appendix I). Elsewhere in North America, Oelke (1966, 1967a,b,c,d) conducted breeding censuses in pine forests of various ages in Ontario and in North Carolina. The unequal spacing of age classes of stands makes direct comparisons difficult. In Ontario, both density and biomass were highest in the youngest stand (18 years) and lowest in the most mature (105 years) stand; in North Carolina, density and biomass were higher in a 5 year stand than in 15-45 year stands, but were greatest in a 75 year stand. Martin (1960) conducted a more general study of succession in Algonquin Park, Ontario, reporting that coniferous stages of succession supported higher breeding populations than deciduous stages, although the numbers of breeding species did not differ. Along the successional series of plant community-types, most bird species showed affinities to coniferous or to deciduous habitats, but did not respond to community changes within these major vegetation types. In a similar vein, Alexander (1973) suggested that many of the species present among a series of altitudinally-distributed seres in the North Carolina Smokey Mountains were broadly distributed, major differences existing only between deciduous and coniferous-dominated stands.

Thus it appears that bird populations, responding in their selection of breeding habitat to features of vegetation structure, may change with major structural changes during forest succession (as from deciduous to coniferous stands). During transitions, when elements of both habitat types are intermixed, species characteristic of both types may be present, leading to an increase in species numbers, density, and biomass. In many local areas, however, successional seres are often assorted in patchy mosaics, reflecting the intermittent nature of past disturbances, so that clear patterns in avian distributions and responses are blurred. Still, some management implications seem clear: if high avian community diversity, density, and biomass are desired, forests should probably be managed to maintain transitional stages or mixtures. Clear-cutting and even-age management probably do not contribute to such ends. While it is tempting (and commonplace) to suggest that these "high diversity" avian communities may also be most stable, and therefore play the most predictable roles in coniferous ecosystems (see below), such conclusions are without factual or theoretical support, and may be dangerously misleading.

Effects of Habitat Alterations

Coniferous forests are subjected to a variety of alterations, most of them resulting from man's intentional or unintentional activities. Some, such as clearcutting, effectively remove the forest, and understandably produce major changes in avian populations and communities. Other alterations are less massive, however, and may be expected to have more subtle effects. Chief among such manipulations are clearing of underbrush, controlled or uncontrolled burning, and spraying of various pesticides for control of insect populations.

Several selected studies may be used to demonstrate some effects of such alterations. Hagar (1960), for example, analyzed the changes in avian communities during the reforestation following clearcutting of douglas fir forest in northern California (site 33 of figure 1). Logging of course altered forest structure, and thus bird species composition, and produced an initial decrease in total density. Within a year, however, breeding densities equaled pre-cutting densities, and three years following cutting, densities exceeded those recorded in mature forests in the area. Avifaunal differences between pre-cut forests and brush stages of cutover regeneration were least in the breeding season, while fall and winter densities in logged areas were 2-3 times those in forests. Logging especially favored granivorous species, such as juncos and Mountain Quail, a shift in ecological composition which may be important in reforestation processes (see below).

Uncontrolled burning (i.e., forest fires) may promote avifaunal changes parallel to those following logging. Bock and Lynch (1970) compared burned and unburned Jeffrey Pine-white fir stands in the Sierra Nevadas (site 36 of figure 1) 6-8 years after an intense fire. Breeding avifaunas on the burned areas were slightly richer in species and more diverse than in unburned forests, probably because of the greater vegetational heterogeneity ("edge") of the burned plots. Breeding densities were similar in both types, but standing crop biomass was greater on the burned area. Foliage-searching birds predominated in the unburned forest, while brush-ground feeding forms were most abundant in burned areas. It seems likely that a shift toward increased granivory also followed burning.

Less intensive cutting or burning predictably has less profound effects on breeding bird communities. In sequoia forests (site 35 of figure 1), Kilgore (1971) reported that clearing

and prescribed burning of understory brush and saplings produced changes in the species composition of the avifauna, but not in total standing crop biomass. Clearing primarily affected birds which nested or fed in the ground and brush layers, but overall this was the least important layer in these forests.

Spraying of various pesticides for insect control may be expected to have less apparent effects upon bird communities, since the forest physiognomy remains largely unaltered. It is difficult to measure direct or especially indirect effects of spraying on breeding bird populations, partly because of the difficulty of recovering dead or sick individuals or of detecting dispersal movements, partly because losses may be rapidly replaced from "floating" populations, at least in some situations (Stewart and Aldrich 1951, Hensley and Cope 1951). Fowle (1965) and McLeod (1967) conducted careful studies of bird populations following spraying of phosphamidon (2-chloro-2-diethyl-carbamoyl-1-methylvinyl-dimethyl phosphate) to control spruce budworm (*Choristoneura fumiferana*) or jack-pine sawfly (*Neodiprion swainei*) populations in New Brunswick and Quebec, respectively. In the New Brunswick study, phosphamidon was applied over 161,000 acres (65,156 ha) at a rate of 0.45 lbs of phosphamidon in 0.75 gal water per acre. Fowle found numerous dead or "sick" birds on census plots soon after spraying, and suggested from cage experiments that the birds somehow accumulated the pesticide from sprayed vegetation in the first few hours following spraying rather than from direct application. Density indices of many species were strikingly reduced following spraying, and did not return to their pre-spray levels before the end of that breeding season. In McLeod's area, phosphamidon was applied at a rate of 0.25 lb in 0.2 gal water per acre over 135,000 acres (54,634 ha) of jack-pine forest. Post-spray censuses recorded substantial reductions in bird populations and dissolution of foraging flocks. Warblers, notably Myrtle Warblers, appeared to be most severely affected by the spraying treatment.

Pesticide spraying at the levels employed in these studies thus undoubtedly reduces bird populations, at least proximately. How long these effects persist is unclear. Neither Fowle nor McLeod suggested the elimination of chemical control of insect populations, but both noted that application rates substantially lower than those commonly used would probably be just as effective in insect control but have reduced effects on bird populations. Recent legislation has, of course, sharply reduced the use of chemicals in insect control in coniferous forests. Still, these effects should be considered in framing management strategies,

especially in those regions in which warblers, which seem particularly sensitive to spraying, are important (figure 5).

ENERGY FLOW

Several processes act to link bird populations and communities in coniferous forests to the forest environment and other components of the forest system. Within an ecosystem context, energy flow is frequently considered to be the most important linkage. To a large extent, this view may stem from the historical definition of ecosystems in terms of trophic dynamics, and current efforts to define ecosystems only in terms of energy flow pathways may prove rather short-sighted. Still, energy flow magnitudes and pathways must be considered a major element of the interrelations of coniferous forest birds with their environments, since it is through these pathways that food consumption patterns and predator-prey dynamics are determined.

Measuring energy flow through forest bird populations and communities, however, is by no means as straightforward as measuring density relationships (which is itself no easy task). Recent attempts to estimate the energetics of breeding populations or communities (Karr 1971, Holmes and Sturges 1973, Wiens and Innis 1973, 1974) have relied upon indirect means. Wiens and Nussbaum (1975) have applied the simulation modeling approach of the latter authors to breeding bird communities in western Oregon coniferous forests, and it is upon that study that the following comments are based.

Model Structure

The structure, logic, and assumptions of the simulation model we employed have been detailed elsewhere (Wiens and Innis 1973, 1974, Innis et al 1974) and will not be reviewed here. The model is founded on the rationale that by combining information on various life history attributes of populations (e.g., clutch size, hatching success, population density) reproductive phenology, and individual bioenergetics (daily costs of existence metabolism, activity, egg production, and growth, modified to account for digestive efficiency) one may obtain approximations of the daily energy demands which individuals and populations (or assemblages of coexisting populations) place upon the ecosystem. In the study of Wiens and Nussbaum (1975) calculations were restricted to the breeding season (1 April - 7 October).

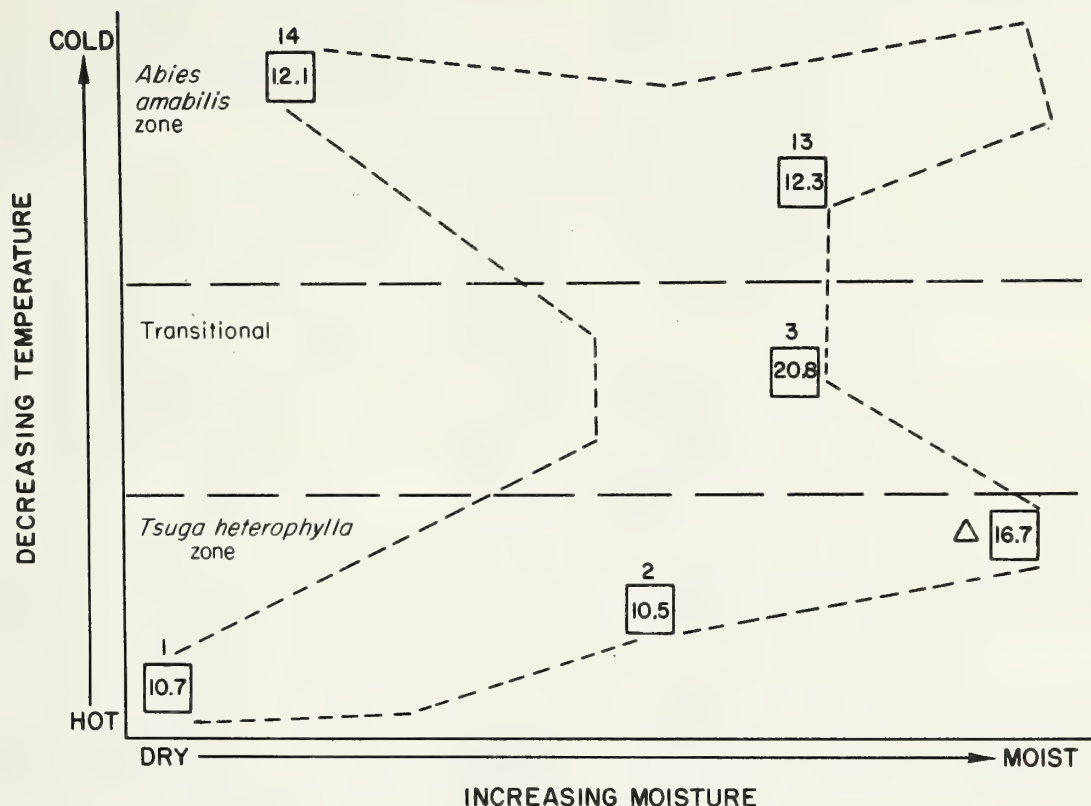


Figure 7.--Estimates of breeding season energy flow (values in boxes, in $\text{kcal m}^{-2} \text{ season}^{-1}$) through bird populations of six coniferous forest stands in the Cascade Range of western Oregon. Positions of boxes indicate the relative location of the six stands (stand symbols next to boxes; see text) in an ordering of central Oregon cascade plant community types by moisture and temperature levels. Dashed line encompasses the range of community types represented in the ordination. From Wiens and Nussbaum (1975).

Energy Flow Magnitudes and Patterns

The model analyses of energy flow in Oregon coniferous forests were derived from breeding censuses conducted in six stands (Appendix I) arranged along gradients of temperature and moisture (figure 7). Three stands (stands 1, 2 and Delta) were warm, low elevation stands dominated by douglas fir (stand 1) or western hemlock (stands 2 and Delta). Stand Delta was located in a river floodplain and was considerably more mesic than the other stands. A third stand (stand 3) was at intermediate elevation and was transitional between the western hemlock and silver fir community

types. The two remaining stands were located at higher elevations but on different slope exposures. Stand 13 was dominated by douglas fir and noble fir, while stand 14, with a dryer microclimate, was dominated by mountain hemlock, noble fir and pacific silver fir.

Estimates of the total energy demand of the breeding communities over the entire breeding season varied considerably among these stands (figure 7). The two low-elevation moderately xeric stands (1 and 2) had the smallest seasonal energy flows, $10.6\text{--}10.9 \text{ kcal m}^{-2} \text{ season}^{-1}$, while the bird populations of the two high-elevation stands (13 and 14)

processed roughly 17 percent more energy (12.5-12.7 kcal m⁻² season⁻¹). Avian community energy demand was considerably higher in the transitional stand (3), roughly twice that of the low-elevation communities. The mesic floodplain stand (Delta) populations had a collective seasonal energy demand of 16.9 kcal m⁻², considerably greater than other stands supporting the same number of breeding species in more xeric locations. Over the range of stands, approximately 1 percent of the seasonal energy flow was channelled into production, while reproduction-related processes accounted for 15-16 percent of the total energy intake. Thermoregulation required 13-19 percent of the seasonal total, with the higher relative costs associated with the cooler, higher elevation stands.

In some respects, peak daily energy consumption may be more important than total seasonal energy consumption, since large daily peaks presumably have more significant effects upon prey populations. The simulation model estimates energy demands on a daily basis, and the analysis of these six Oregon stands indicated well-defined peaks of community energy demand at all sites. Peak daily energy demands varied from 0.08-0.15 kcal m⁻² day⁻¹, with the highest values recorded in stands 3 and Delta.

These patterns of energy flow are of theoretical interest, but of greater immediate importance are the ways in which energy flow is expressed in consumption of prey organisms. The model estimates of energy demands may be converted to estimates of food consumption rates by combining information on the dietary habits of the bird populations with information on the caloric values of various prey taxa. Detailed information on food habits was not available for many of the species breeding in these Oregon stands, so we considered the composition of the diet in terms of either animal or plant prey types, an admittedly crude approximation of actual dietary composition. In all stands most of the energy was obtained from animal prey sources (figure 8). The percentage of the total seasonal energy intake derived from animal sources varied from 71 to 84 percent among all stands except stand 14 (the high elevation xeric site), where less than 60 percent of the energy was drawn from animal sources. Over the range of stands we calculated that the breeding bird communities consumed 3.1-6.9 g m⁻² season⁻¹ of invertebrate prey and 0.7-2.2 g m⁻² season⁻¹ of seed prey. Values such as these of course, are not very meaningful unless coupled with concurrent estimates of the availability (standing crop) of invertebrate or seed prey types. Unfortunately such data are not available from these study locations, and even if they were, interpretation of the relationships

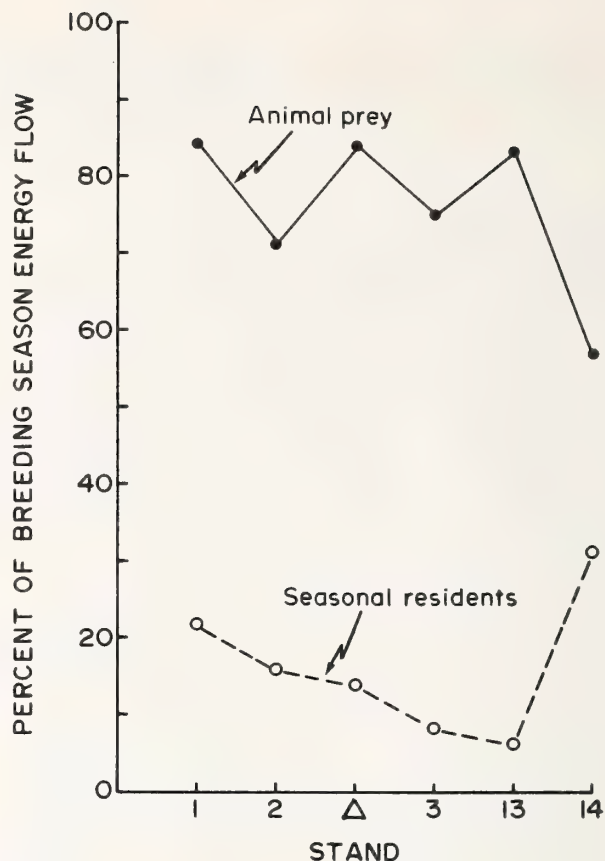


Figure 8.--Percentages of estimated total avian community breeding season energy intake in six western Oregon coniferous stands (see text) derived from animal prey sources (above), or consumed by seasonal resident (i.e. migratory) bird species. From Wiens and Nussbaum (1975).

would be difficult, since so much depends upon the various factors influencing prey selection behavior of the avian predators. Precise estimation of energy flow from food compartments or food consumption rates requires knowledge of the population dynamics and density of individual bird species, their prey preferences given varying states of prey availability, and the potential availability of prey organisms to the birds. Information of this sort is not available for any population of coniferous forest species and in the absence of such detailed data this simulation modeling approach at least provides a means of generating crude estimates of community energy and food consumption.

The simulation model may also be used to assess the ecological structuring of breeding avifaunas in terms of energetics rather than individual densities. Species were categorized according to foraging station and general dietary

habits in a manner similar to that employed in the above community analyses. Foliage-gleaning forms accounted for the greatest proportion of the seasonal energy intake at all stands except stand 2, where ground-feeding forms consumed a slightly greater percentage of the total energy flow (figure 9). Insectivorous species predominated among the foliage-feeders at all stands except stand 14, where plant-feeding species which were generally restricted

to the higher elevation stands accounted for the greatest proportion of the total energy flow. Air-foragers were virtually absent from these higher-elevation stands and contributed only a small portion of the energy flow elsewhere. Ground-feeding species generally decreased their proportionate share of total community intake from stands 2-14. Categorizing species by their length of tenure in the stands (as seasonal or migratory vs. permanent residents) revealed

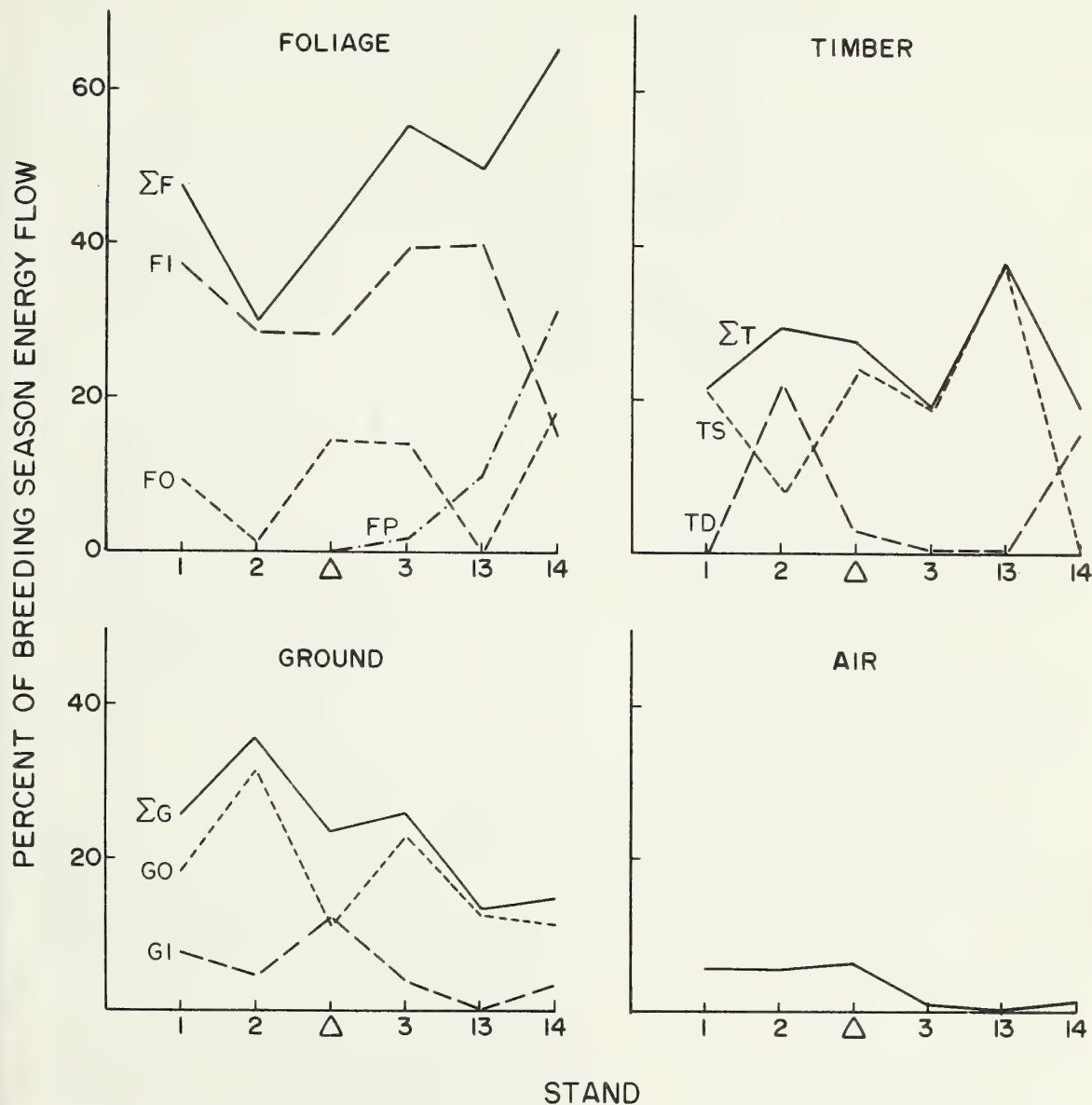


Figure 9.--Partitioning of estimated total avian breeding season energy flow in six western Oregon coniferous forest stands (see text) among ecologically-defined segments of the avifauna. FP = foliage plant (seed) feeders, FO = foliage-feeding omnivores, FI = foliage insectivores, TD = timber drillers, TS = timber searchers, GI = ground-feeding insectivores, GO = ground-feeding omnivores. From Wiens and Nussbaum (1975).

that the proportion of the total community energy intake consumed by seasonal residents decreased steadily from the dryer low-elevation stands to the more mesic and higher-elevation stands (figure 7). This stand sequence reflects a shortening of the growing season, later persistence of low temperatures (and attendant retardation of insect emergence), and generally more severe environmental conditions persisting later into the breeding season. Under such conditions the seasonal "flush" in insect abundance which is generally exploited by migratory species may become increasingly restricted in time, favoring the more flexible resident species. In the dry highest elevation stand (14) seasonal residents accounted for a greater proportion of the total energy flow than in any other stand. This was accompanied by a change from dominance by insectivorous forms to seed- and fruit-eating species among the foliage feeding group (figure 8) and a general reduction in the percent of breeding season energy flow obtained from animal prey (figure 7). These patterns suggest that as environmental conditions during the early portion of the breeding season worsen with increasing elevation and/or dryness, a point is reached at which even the resident species may find it difficult to exploit the system, and highly opportunistic plant-feeders may be able to utilize the resources more effectively. Evening Grosbeaks and Red Crossbills, two seed-eating species known for their "irruptive" and opportunistic population movements, together accounted for 40 percent of the energy flow in stand 14. Such species were generally absent from other stands.

West and DeWolfe (1974) used an approach to estimate breeding season energy demands which is similar but simpler than the simulation model approach. For a Taiga forest in Alaska (site 29 of figure 1), they estimated a consumption of roughly 7.0 kcal m^{-2} by the breeding bird communities (adults only) over a 99-day breeding period. If this estimate is doubled to equate it with the breeding "season" considered in the Oregon simulations, and that value then increased by roughly 15 percent to account for production, an estimated seasonal energy flow of roughly $15.5 \text{ kcal m}^{-2} \text{ season}^{-1}$ is obtained, which falls well within the range of values from the Oregon simulations.

Relatively few other analyses are available with which these patterns and magnitudes of breeding season energy flow may be compared. Wiens and Nussbaum (1975) compared their estimates with those derived by Holmes and Sturges (1973) and by Karr (1971) using quite different approaches. A more straightforward comparison may be made of these coniferous forest values with estimates of breeding season energy flow

through grassland bird communities obtained using the same simulation model (Wiens and Dyer, this symposium). Among a range of grassland situations, breeding avifaunas consumed from $0.9\text{--}2.9 \text{ kcal m}^{-2} \text{ season}^{-1}$ over a breeding season one month shorter than that of the coniferous forests. Thus, while standing crop biomass in breeding coniferous avifaunas is only two to three times that in grasslands, energy flow is nearly ten times as great. To a large degree this may reflect the greater degree of dominance of extremely small species, forms which have relatively high energy demands per unit body weight in comparison to the larger species common in rangelands.

One other approach to determining energy flow relationships through coniferous forest avifaunas has been advocated by Salt (1957). Salt suggested that standing crop biomass figures represented a biased portrayal of community structure, since different-sized species differ in their metabolic efficiency and therefore their role in community energetics. Salt calculated "consuming biomass" values by multiplying density by body weight to the 0.7 power for each species, in recognition of the relatively lower metabolic rate per gram body weight of larger species. Salt suggested that the ratio of consuming biomass to standing crop biomass of a community (CB/SCB) may be a measure of efficiency in food utilization, since communities dominated by large species which require less energy per gram of body weight exhibit a greater discrepancy between consuming and standing crop biomass. Salt analyzed breeding avifaunas in Wyoming coniferous forests and concluded that there was an increase in community energetic efficiency (as measured by the ratio of consuming biomass to standing crop biomass) as succession proceeds towards the climax. Karr (1968) defined similar relationships for successional stages of Illinois strip-mine habitats, and Kilgore (1971) observed similar directional changes in undisturbed sequoia forests in the Sierra Nevada. In the experimental plots in Kilgore's study the ratio of consuming to standing crop biomass decreased, suggesting to him a slight reversal of the successional process. On the other hand, Bock and Lynch (1970) using this approach projected a greater efficiency in energy processing on burned than unburned forest plots in the Sierra Nevada. They suggested that foraging options differed in the burned and unburned plots, favoring larger ground- or brush-feeding forms in the burned plots and smaller foliage insectivores in the unburned plots. Thus, while the flow channels of energy in the burned and unburned forests differed, total community energy flow may not have varied much. Regression analyses of

standing crop biomass, consuming biomass, and CB/SCB ratios for the six stands of Wiens and Nussbaum (1975) in relation to model-derived estimates of energy flow suggest a slightly better fit with consuming biomass than with standing crop biomass ($r = 0.977$ and 0.916 , respectively), but this leaves unresolved the question of how well the CB/SCB ratio actually portrays "community efficiency".

THE ROLE OF BIRDS IN CONIFEROUS FOREST ECOSYSTEMS

Bird populations or communities are tied into the functional framework of coniferous forest ecosystems in a myriad of ways, and their "importance" in the system may thus be gauged in ways other than energy flow or even total food consumption rates (e.g., Sturges et al. 1974, Wiens and Dyer this symposium). While our knowledge of many of these system-related roles is meagre, a number of studies have rather directly addressed the role of bird populations in specific predator-prey relations in coniferous forests. These studies have been economically rather than theoretically motivated (although their contribution to theory has been substantial), and have been primarily concerned with the relations of bird populations to various insect prey dynamics (e.g. spruce budworm, Englemann spruce beetle), or to seed resources in relation to reforestation processes. Among the insectivorous forms, foliage-gleaners (chiefly warblers) and timber-drilling species (woodpeckers) have received greatest attention, focusing on the nature of their responses to changes (increases) in prey density and their potential role in "controlling" rates of increase in prey populations. These studies are thoroughly reviewed elsewhere in this symposium (Thomas et al.)

Insectivorous Predators

Coniferous forests, especially those subjected to management for timber yield, are frequently distributed in large blocks of even-aged trees of few or of a single species. Such forests in many areas are subject to outbreaks of insect pests, such as spruce budworm (*Choristoneura fumiferana*), black-headed budworm (*Acleris variaria*), hemlock looper (*Lambdina fiscellaria*), larch casebearer (*Coleophora laricella*), jack pine budworm (*Choristoneura pinus*), and several others. Foliage-gleaning insectivorous birds are frequently considered to be at the least potentially important predators of such insects (e.g. Otvos and Taylor 1970, Sloan and Coppel 1968, Coppel and Sloan 1970, Mitchell 1952). Estimates of consumption "impact" of the birds (i.e., the percentage of the insect population consumed by avian

predators) vary. Gage et al. (1970) used ingenious methods to estimate that birds consumed between 3 and 14 percent of black-headed budworm populations over a three-year period in New Brunswick, while Sloan and Coppel (1968) suggested that a 24 percent overwinter decrease in larch casebearer populations in Wisconsin was attributable to birds, and that spring predation produced a significant additional loss. Lower consumption values (1-7 percent) were reported on spruce budworm populations in Ontario, New Brunswick, and Maine by Kendeigh (1947), George and Mitchell (1948), Dowden et al. (1953), and Morris et al. (1958). Consumption magnitudes thus appear variable, but in no case does it seem that bird predation can effectively "control" insect population density, at least among these "irruptive" prey forms. Avian predation on these defoliating insects is to a large degree density-dependent (Gage et al. 1970, Mitchell 1952), initially involving individual functional responses as prey densities increase from low endemic levels, perhaps through the formation of searching images (Tinbergen 1960, Sloan and Simmons 1973). As prey density increases to epidemic levels, the functional response of avian predators is frequently accompanied by a numerical response in at least several bird species (Kendeigh 1947, Morris et al. 1958). Morris and his colleagues noted especially numerical "outbreaks" in Bay-breasted, Blackburnian, and Tennessee warbler populations following budworm epidemic (figure 10), and suggested that warblers are particularly well-suited to exhibit a numerical response,

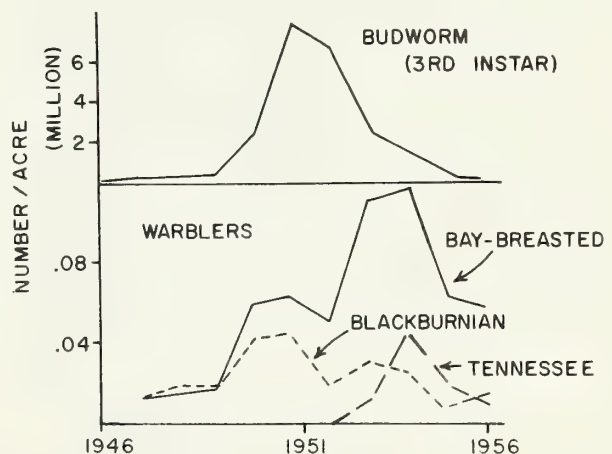


Figure 10.--Population trends in spruce budworm and numerical responses in warblers during a budworm outbreak in New Brunswick. From Morris et al. (1958).

since they are migrants (and thus not subject to local winter limitation) and highly insectivorous foliage gleaners (thus increases in prey density should directly increase the production of offspring). Indeed, warblers appear to form a major portion of the species noted responding functionally and/or numerically to defoliating insect outbreaks (Otvos and Taylor 1970, Sloan and Coppel 1968, Mitchell 1952, MacArthur 1958, Cheshire 1954). Again, the relations between warbler densities and relative densities in various coniferous forests (figure 5) and endemic and epidemic levels of defoliating insects deserves close scrutiny, in view of this predation potential. Avian predation, however, appears to respond to increases in prey density, or perhaps exert some "regulation" on the rate of prey increase, rather than control (in any economic sense) defoliating insect prey. Gibb (1961), speaking of introduced pine forests in New Zealand, provided a succinct statement of the role of avian predators in influencing insect outbreaks:

"With their low reproductive potential, birds cannot cope with plagues of insects once they have broken out; but at the more prevalent endemic levels of their prey they can eat a significant fraction of their food stocks (Gibb 1958, 1960; Tinbergen 1960), and under certain circumstances their predation can dampen down oscillations in insect numbers which might otherwise develop into serious outbreaks (Tinbergen & Komp 1969)." (It should be noted in passing that not all potentially epidemic defoliating insect populations are subject to even low-level "regulation" by avian predators. Thus birds consume extremely few tent caterpillars (*Malacosoma constrictum*), even during population outbreaks, apparently because the integumental hairs of the caterpillars render them unpalatable to the birds (Root 1966).

Woodpeckers of several species apparently exhibit relationships to population fluctuations of bark beetle prey which parallel those of foliage-gleaning insectivores and defoliating insects. Their role seems especially important (or has received intensive study) in Rocky Mountain forests, where Englemann Spruce beetles (*Dendroctonus obesus*) frequently infest wind-thrown spruce trees and logging slash. In such areas, Northern three-toed Woodpeckers, Hairy Woodpeckers, and Downy Woodpeckers are the most important avian predators on the beetles (Koplin 1969, 1972, Amman and Baldwin 1960, Baldwin 1960). These woodpeckers, especially the Northern three-toed, respond both functionally and numerically to outbreaks of spruce beetles in localized areas. Of the three woodpecker species, only the Northern three-toed is closely associated in its foraging with recently dead spruce trees, and thus at endemic prey

levels it is chiefly this species which contributes to mortality of the beetles. As prey densities increase to epidemic levels all three species increase their consumption rates, so that at "pan-epidemic" levels spruce beetles are essentially the only prey taken, and the magnitude of functional response is thus limited by stomach capacity (Koplin 1972). Since Hairy Woodpeckers have the largest stomach, they exhibit the greatest maximum functional response (Jackman 1975).

Numerical responses may play a larger role in determining woodpecker impact on spruce beetle populations, especially at non-endemic levels. Woodpeckers frequently disperse or "drift" from breeding localities during the fall, and may thus form aggregations as they encounter localized foci of beetle infestations (Baldwin 1968a, Koplin 1972). In Colorado, increases in beetle populations from endemic to epidemic levels produced as much as a fifty-fold increase in woodpecker density (Koplin 1969, Amman and Baldwin 1960, Baldwin 1960), with density increases most pronounced in Northern three-toed and least pronounced in Downy Woodpeckers. At high prey densities, however, numerical responses fail to keep pace with prey density increases, apparently because of limits to packing of breeding territories (Koplin 1972). This, of course, imposes an upper limit on nesting density, and thus on reproductive output (Baldwin 1968a).

Functional and numerical responses interact to determine the "impact", or percentage loss from the prey population to predation, of the woodpeckers on prey levels. At moderate to high beetle densities, woodpeckers may consume from 24 to 98 percent of the beetle population (McCambridge and Knight 1972, Baldwin 1960, 1968b, Koplin 1972), while consumption at endemic levels is generally lower, on the order of 2 to 26 percent (Koplin and Baldwin 1970). Baldwin (1968a), summarizing Koplin's studies, reported that woodpecker predation in Colorado Englemann Spruce windthrows accounted for 28 percent of the beetle mortality at endemic levels (400-1000 beetles/acre), 84 percent mortality at epidemic levels (160,000 beetles/acre), and 53 percent mortality in pan-epidemic (1,600,000 beetles/acre) populations. Thus woodpecker predation may be most severe at epidemic levels, but a very dense outbreak of beetles can swamp out the pressure of woodpecker consumption (Koplin 1972, Jackman 1975). Koplin (1972) developed a deterministic model to predict beetle consumption levels as a function of woodpecker food requirements, stomach capacity, population density, and air temperature which closely matched these recorded consumption values.

Woodpecker consumption of beetles is patchy in time and space, which to a large degree reflects the heterogeneity of insect population levels over a large region. Shook and Baldwin (1970) analyzed the degree of woodpecker consumption of spruce beetles in open, semi-open, and dense forest stands in Colorado. Overwinter reduction of the beetle brood was approximately 50 percent in all areas, but by the following fall, populations had been reduced by 71, 83, and 52 percent, respectively. Spruce beetle density was apparently greatest in semi-open forests, likely promoting a somewhat greater numerical response there than elsewhere. In sum, woodpecker predation may play a role in controlling local outbreaks of spruce beetles at moderate levels, but is probably largely ineffective in preventing epidemics or pan-epidemics over larger areas (Koplin 1972, Koplin and Baldwin 1970).

Woodpeckers, of course, are not the only avian predators to respond to outbreaks of spruce beetles in the Rocky Mountains. Baldwin (1968a) suggested that Olive-sided Flycatchers, Mountain Chickadees, Mountain Bluebirds, Gray-headed Juncos, and several other passerine species may have consumed as much as 24 to 32 percent of the emerging beetle population at moderate beetle density levels in Colorado. These passerines were largely opportunistic in their feeding responses, however, and fed upon only the emerging stages; their potential impact may thus be far less than that of woodpeckers, which feed over a broader span of beetle life-stages.

Granivorous Predators

Birds may also play a potentially important role in the dynamics of coniferous forest ecosystems through their consumption of seeds and/or seedlings of forest trees. These effects may at time become economically important, especially in relation to reforestation of cut-over areas, whether through natural seed-fall or artificial seeding. Several studies in western coniferous forests (Hagar 1960, Eastman 1960, Gashwiler 1967, 1970, Noble and Shepperd 1973) have suggested that granivorous species may pose potentially serious problems in reforestation efforts. Hagar (1960), for example, calculated a potential consumption of 17 percent of the maximum seedfall during a good year by juncos, while Gashwiler (1970) estimated that birds and chipmunks (probably mostly birds) destroyed 24 percent of the available conifer seeds (primarily douglas fir) between fall and the end of the germination period the following year. In Colorado Engelmann spruce habitats, Gray-headed juncos may account for clipping of

up to 20 percent of the newly-germinated spruce seedlings, and are the second leading cause of first-season mortality in clearcut openings (Noble and Shepperd 1973). Juncos frequently appear to be the major species involved in consumption of douglas fir seeds in reforestation, although Mourning Doves, Song Sparrows, White-crowned Sparrows, Varied Thrushes, Fox Sparrows, Rufous-sided Towhees, and Golden-crowned Sparrows may also contribute to seed loss in some areas (Hagar 1960, Gashwiler 1967, Eastman 1960). Juncos, of course, are among the most abundant and broadly-distributed species of coniferous forests in North America (table 1). Peak abundances of granivorous birds, however, frequently do not coincide with peak availability of seed crops (in late fall); most of the losses may occur in spring, as the seeds germinate (Gashwiler 1970). Since most of these granivorous species are dietary opportunists, they may respond to increases in alternate foods, a management possibility suggest by Hagar (1960). Artificial reforestation, however, often involves local increases in "alternate" food sources in open areas, and may well act to attract birds such as juncos to these areas (Noble and Shepperd 1973). Unfortunately, the total impact of avian seed consumption on coniferous forest ecosystem dynamics (or economics) is as yet unclear, which renders management options uncertain at best. The role that avian seed consumption may have in natural thinning of seedlings, for example, has not been explored.

CONCLUDING COMMENTS

The foregoing review of avian breeding communities in North American coniferous forests has revealed a number of characteristic features of these avifaunas. They are, for example, fairly rich in breeding species, with moderate to high densities. In many areas, especially the Northeast, most individuals are small foliage insectivores. These and several other groups have been suggested to exhibit important relationships to prey populations, whether insect or seed. While the major goal of this paper has been to provide background information on avian communities in coniferous forests, several points with direct management implications have become apparent to me during the preparation of this review, and deserve comment.

First, there are several well-defined areas in which research should be given high priority. We know very little of the linkages between avian consumers and the dynamics of their prey populations, and how these relationships are in turn linked to other components of coniferous forest systems. Does consumption

of a moderate portion (say, 25-50 percent) of conifer seedfall inhibit forest regeneration following disturbance? Do birds play a role in seed dispersal and thus enhance natural successional processes? Does the localized thinning of seedlings by birds reduce subsequent competition among saplings and promote growth? How are the patterns of seed consumption by coniferous forest birds related to those of small mammals? What are the real effects of insectivorous birds in extending the time frame of endemic-epidemic oscillations in pest insect populations? What are the roles of alternate food supplies in avian responses to fluctuations in the populations of insects or seeds of economic importance? Unfortunately, our approach to exploring such questions has generally been more inferential than empirical. If we are to assign economic parameters to the management of non-game birds, we will require careful assessment of the true relationships of avian consumption patterns to prey population structure, spatial dispersion, and dynamics.

It is also critical to establish the spatial scales of coniferous forest habitats which are compatible with economic requirements but also insure the continuing balance of native bird populations. At one level, we must determine the sizes the blocks of unbroken forest habitat which are essential to harbor essentially "stable" bird populations. Here the spatial requirements of wide-ranging forms, such as jays, some woodpeckers, and especially forest raptors, may set the limits. What size of forest block is required, for example, to insure continuing reproductive success and survival of a pair of Pileated or three-toed woodpeckers, or a pair of Goshawks? Is our management policy to aim at maintenance of one pair, or two, or ten? What sizes of habitat blocks, defined by the requirements of the wide-ranging species, will also insure success of small foliage insectivore populations, or ground-foragers? These questions are critical, but as yet unanswered. At another level, the pattern of interspersions of habitats within a forested area may be especially critical. Maintenance of "representatives" of various successional seres within an area is increasingly recognized as a management objective, but do we know how such areas should be arrayed with respect to one another? Is it best to maintain an old-growth stand adjacent to a clear-cut, or to a shrub stage, or to an even-age or multi-age stand? What sort of internal heterogeneity should managed stands possess? Surely even-age monocultures with even spacing of trees, no spaces in the canopy, and no snags must represent a structurally sterile habitat, and the inclusion of snags, or air-spaces within the canopy, or patches of non-managed tree species in a stand may render a forest block much more attractive to a broader variety of characteristic

coniferous forest species. I consider definition of these spatial influences on bird populations to be our most pressing research priority.

A second point relates in a sense to the dimensions of non-game bird management. Should management objectives be aimed at or based upon single species populations or upon assemblages or "suites" of species? Should habitat management strive to maintain populations or assemblages of "native" species, or "economically important" species (such as, perhaps, insectivores---Warblers, woodpeckers, flycatchers, etc.), or some other complement of species? To me, the goal seems clearly to be management of habitat for the continued success of suites of species which are characteristic of coniferous forests of various sorts (i.e., the moderate to high-frequency species of table 1). This sort of management, however, must not be incompatible with the management of single species populations which merit special attention, such as Spotted Owls in old-growth stands in the Pacific Northwest (Meslow and Wight, this symposium), or Red-cockaded Woodpeckers in Southeastern pine forests (Thompson 1971). Frequently, carefully-considered management for such "special" species, or for "indicator" species (i.e., habitat specialists), may also insure proper management for natural species assemblages. Multivariate approaches to habitat analysis (e.g., Shugart, this symposium, Anderson and Shugart 1974) may provide a valuable tool in defining the habitat relations of specialist species and their broader linkages to suites of other coniferous forest birds.

A final point relates to the use of measures of "diversity" in framing management approaches. When land managers speak of managing for maximum diversity it is often unclear whether they have habitat diversity or avian diversity (or some combination of the two) in mind. The comments offered above on habitat interspersions relate to habitat diversity: the maintenance in a given management area of a broad sampling of suitably-sized and spatially arranged units of vegetation types (e.g., successional seres). Properly pursued, this is a valid and important management objective. Management for the maintenance of high bird species diversity, however, is another matter. Diversity is normally measured with one of several indices (see Balda, this symposium), most of which consider the number of species present as well as their relative densities. At times it is suggested that the more diverse communities may also be the most stable. Such inferences are unfounded, and have dangerous implications in management programs which aim at achieving stable systems. Further, a measure of diversity in itself, or even compared with diversity measures from other habitats or systems, is virtually worthless as

a management tool. Diversity measures are extremely sensitive to the area sampled and the internal heterogeneity of that area. Thus diversity may be increased by partitioning habitat units in an area into small blocks which may increase species numbers and perhaps lead toward greater equitability in species abundances, while at the same time reducing population sizes to perhaps dangerously low levels, especially among the more wide-ranging forms. Further, the effects of increasing species number and increasing equitability are intertwined in many diversity measures (although not in all), and thus the factors responsible for high diversity are not always clear. But the greatest failure of diversity measures, in a management context, is their qualitative insensitivity, their failure to consider which species or which sorts of species are contributing to changes in diversity accompanying management. Willson (1974) has argued that proper understanding of the structure and organization of natural avian communities (and thus intelligent management) must be based upon careful studies of meticulously delineated species assemblages, resource relationships, reproductive success, and events in the nonbreeding as well as the breeding season rather than upon correlative approaches relating avian diversity to arbitrary divisions of habitat structure. If our objective is habitat management for natural wildlife (game and non-game) populations and assemblages, rather than for an abstract measure of "diversity", Willson's comments must define our ultimate approach.

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Appendix I.--Features of breeding bird communities in North American coniferous forests, as calculated from census results.
Site numbers refer to the codes in Figure 1.

State or Province	Site No.	Forest Type	No. Samples	No. Species	Density ² (indiv./km ²)	Standing Crop Biomass (g/ha)	Dominance		Reference
							1 species	2 species	
NORTHWEST IMMATURE									
New Brunswick	1	Jack Pine	1	17	317.5	76.9	27	48	Erskine 1969a
	3	Balsam Fir	3	9	361.2	47.2	22	39	Gage et al 1970
Quebec	6	Jack Pine	1	12	164.7	28.1	26	38	Erskine 1970a
	"	Black Spruce	1	14	405.5	59.2	19	38	Erskine 1970b
	8	Jack Pine	3	7	234.0	45.1	37	60	McLeod 1967
Ontario	10	Black Spruce	1	15	463.3	76.8	23	42	Erskine 1972a
	"	Jack Pine	1	11	175.5	31.6	18	34	Erskine 1972b
	11	Semi-Open Pine	1	6	617.8	190.3	27	54	MacDonald 1965
	13	Pinus strobus	1	9	217.4	32.6	45	59	Martin 1960
NORTHWEST MATURE									
New Brunswick	2	Fir-Spruce	1	32	1129.3	202.3	20	26	Erskine 1969b
	4	Red Spruce	1	27	1395.3	259.5	13	23	Erskine 1969c
	5	White Cedar-Balsam Fir	1	23	2131.5	289.5	12	21	Tull 1973
Quebec	7	Fir-Spruce-Alder	1	26	873.9	122.3	13	21	Erskine 1970c
Ontario	9	15-20 yr Red Pine	1	19	1795.3	583.8	20	37	Oelke 1967a
	"	85-95 yr White Pine	1	25	1361.8	342.3	10	19	Oelke 1967b
	"	100-110 yr Pitch Pine	1	18	1324.5	316.8	17	30	Oelke 1967c
	"	100-110 yr Hemlock-Pine	1	18	1331.4	318.4	17	31	Oelke 1967d
	11	Mixed Red Pine	1	18	1779.1	622.7	25	33	MacDonald 1965
	13	Picea mariana	1	19	924.2	63.4	14	20	Martin 1960
	"	Picea-Thuja	1	24	1082.3	89.9	12	18	"
	"	Abies-Picea	1	20	1186.1	228.2	23	38	"
	"	Abies-Picea	1	23	1245.4	192.0	13	25	"
	"	Tsuga	1	26	1344.2	216.8	38	48	"
Maine	14	Abies-Picea	2	26	1865.6	302.5	23	37	Slewart & Aldrich 1951, Hensley & Cope 1951
Vermont	15	Red Spruce	1	19	1131.3	206.5	26	37	Nichols 1968

State or Province	Site No.	Forest Type	No. Samples	No. Species	Density 2 (indiv./km ²)	Standing Crop Biomass (g/ha)	Dominance		Reference
							1 species	2 species	
NORTHWEST MATURE									
Connecticut	16	Hemlock-White Pine	3	26	1201.9	347.2	13	24	Magee, 1968, 1969, 1970
New York	17	Red Pine-White Pine	2	18	1028.1	208.3	27	45	Klingensmith 1970, 1972
SOUTHEAST									
West Virginia	18	Spruce	2	14	876.4	212.8	31	55	Sigel et al 1968, DeGarmo et al 1973
"	19	Fir-Spruce	1	20	1874.7	272.5	21	34	Brush et al 1973
"	20	Fir-Spruce	1	19	1245.4	177.8	12	22	Hutton et al 1968
Tennessee	21	Spruce-Fir	1	13	1400.2	226.8	27	45	Alsop 1969
North Carolina	22	1-10 yr Pine	1	25	1228.4	365.4	23	38	Oelke 1966
"	"	10-20 yr Pine	1	20	921.0	271.9	14	26	"
"	"	20-30 yr Pine	1	25	975.9	275.3	28	47	"
"	"	30-40 yr Pine	1	24	857.0	246.3	17	32	"
"	"	30-60 yr Pine	1	31	888.4	253.2	14	26	"
"	"	70-80 yr Pine	1	25	1938.9	511.9	18	29	"
NORTHERN									
Ontario	12	Mature Spruce-Fir	3	26	556.7	128.6	12	20	Sanders 1970
"	"	20-yr Spruce Fir	3	24	633.8	142.2	12	25	Sanders 1970
Saskatchewan	23	Black Spruce	1	16	425.7	68.0	21	39	Erskine 1973
"	24	Balsam Fir	1	18	719.6	110.9	17	32	"
Northwest Terr.	28	Black Spruce-Jack Pine	5	9	517.9	101.4	31	49	Carbyn 1971
Alaska	29	Black Spruce	2	15	199.8	41.0	20	37	West & DeWolfe 1974
ROCKY MOUNTAIN									
Colorado	38	Ponderosa-oak	4	11	883.4	276.4	43	56	Snyder 1970, 1971, 1972, 1973
"	39	Ponderosa-Douglas-Fir	1	14	513.0	104.0	35	52	Snyder 1950
"	"	Lodgepole Pine	1	13	301.9	72.8	38	59	"
"	"	Spruce-Fir	1	12	452.2	83.6	31	58	"
"	40	Lodgepole Pine	3	11	322.0	69.1	25	41	Kingery 1970, 1972, 1973
"	41	Ponderosa	1	20	474.4	163.6	13	22	Hering 1948
"	42	Ponderosa	1	13	1334.3	422.3	24	39	Hering 1973

State or Province	Site No.	Forest Type	No. Samples	No. Species	Density 2 (indiv./km ²)	Standing Crop Biomass (g/ha)	Dominance		Reference
							1 species	2 species	
ROCKY MOUNTAIN									
Colorado	43	Ponderosa-Douglas Fir	5	22	458.6	---	---	---	Winternitz 1973
	44	Lodgepole-Spruce	1	14	528.8	103.5	23	40	Webster 1967
Wyoming	45	Lodgepole	1	8	180.4	48.3	26	46	Salt 1957
	"	Lodgepole-Spruce Fir	1	14	482.8	157.8	19	37	"
Montana	"	Spruce-Fir	1	19	529.3	225.2	19	31	"
	46	Douglas-Fir-Lodgepole	1	10	890.5	125.8	13	26	Fissell 1973
	"	Ponderosa-Douglas Fir	1	20	950.0	198.6	27	42	Manuwal 1968
	"	Lodgepole-larch-Douglas Fir	1	20	905.4	204.1	17	32	"
Utah	47	Spruce-Fir	2	23	2663.1	610.6	12	22	Burr 1969
Oregon	32	Fir-Pine-Spruce	1	14	639.4	143.1	30	48	Archie & Hudson 1973
SIERRA NEVADA									
California	34	Red Fir-Lodgepole	1	14	759.1	154.9	16	29	Robert 1966
	35	Giant Sequoia Control	3	27	1198.4	516.5	13	24	Kilgore 1971
	"	" " Treatment	3	22	1399.8	534.9	14	25	"
	36	Jeffrey Pine-White Fir Burn	3	22	449.7	131.2	21	38	Bock & Lynch 1970
"	" " unburned	3	17	447.3	72.8	21	40	"	
NORTHWEST COASTAL									
British Columbia	25	Hemlock-Cedar	1	18	1005.7	251.0	15	27	Webster 1969
	26	White Spruce	1	23	1065.0	194.5	20	30	"
	27	White-Spruce-Alpine Fir	1	28	1587.4	278.3	21	32	Grant 1966
Oregon	30	Douglas Fir	1	12	1779.0	262.8	22	42	Wiens & Nussbaum 1975
	"	Hemlock-Douglas Fir	1	12	1380.0	275.8	21	34	"
	"	Hemlock-Maple	1	12	2619.0	424.3	21	41	"
	"	Hemlock-Sliver Fir	1	15	2887.0	526.1	24	48	"

State or Province	Site No.	Forest Type	No. Samples	No. Species	Density 2 (indiv./km ²)	Standing Crop Biomass (g/ha)	Dominance		Reference
							1 species	2 species	
NORTHWEST COASTAL									
Oregon	"	Douglas Fir-Noble Fir	1	7	1910.0	223.3	23	41	"
	"	Mountain Hemlock	1	13	1229.0	361.9	21	39	"
	31	DF ecotone	1	16	1440.6	328.4	11	21	Anderson 1970, 1972
	"	Douglas Fir	5	13	1071.9	227.9	20	34	"
	"	Hemlock ecotone	1	16	1250.3	238.1	22	30	"
California	"	Hemlock	1	7	896.9	94.6	45	58	"
	33	Cutover DF	3	9	647.4	365.6	36	49	Hagar 1960
	"	Douglas Fir	2	13	588.1	148.1	34	49	"
	37	Bishop Pine	4	26	1770.0	323.1	13	23	Long 1971, Stewart & Higbee 1973, Darling 1971, Hansen 1973
	"	Douglas Fir	3	21	1626.7	288.2	18	27	Darling 1971, Milton & Murray 1972, Akers & Hansen 1973

Avifauna and Succession in Douglas-fir Forests of the Pacific Northwest¹

E. Charles Meslow and Howard M. Wight^{2/}

Abstract.--In the Douglas-fir region of western Oregon and Washington, natural succession generally proceeds rapidly through grass-forb and shrub stages to enter a long period of Douglas-fir dominance. Climax forests of western hemlock and western red cedar are relatively rare but old-growth forests of Douglas-fir, undisturbed for 400-600 years were relatively common. Timber management attempts to speed regeneration and establish an even-aged monoculture of Douglas-fir for harvest at optimal size. We identify the bird species inhabiting five seral stages of these forests and discuss four spheres of influence in which timber management conflicts with forest birds: 1) Shortening of the grass-forb and shrub stage. 2) Effect of an even-aged Douglas-fir monoculture. 3) Elimination of snags. 4) Elimination of old-growth forest.

INTRODUCTION

In 1908, Charles C. Adams rather prophetically stated that "the relation of bird life to forests and forest succession has received little attention....here is a field which, as time advances, will become of more and more importance, and these problems will eventually call for specially trained men to handle them." I suspect that this quotation may be appropriate to our concluding remarks as well. It would seem that despite Adams having alerted us to the need for understanding forest succession-avifaunal relationships some 67 years ago, we have not yet succeeded in documenting the relationships, let alone understanding them.

In choosing to discuss the Douglas-fir (*Pseudotsuga menziesii*) region of western Oregon and Washington, we exclude the great bulk of the coniferous forested area of North America. But then, we devote our attention to an area managed

almost exclusively for timber values; economic stakes are high--100 acres of old-growth Douglas-fir now (1975) sells for about \$1,600,000 on the stump. Obviously, when such values are involved we should expect land management to emphasize optimization of timber production. Conflicts with wildlife, perhaps especially nongame birds, follow as a matter of course.

FOREST SUCCESSION

Our remarks are directed primarily to the coniferous forest systems with which we are most familiar--those of Oregon. Chief among these is the region of Douglas-fir on the west side of the Cascade Range. These Douglas-fir forests are replaced in natural succession by western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) climaxes (Franklin and Dyrness 1973). These western Oregon forests have several unique features:

a) Stands are almost totally dominated by conifer species under natural conditions.

b) The large size and longevity of the dominant species leads to great biomass accumulation.

1/ Paper presented at the Symposium on Management of Forest and Range Habitats for Nongame Birds, Tucson, Arizona, May 6-9, 1975.

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Franklin and Dyrness (1973) review successional patterns in western Oregon and Washington. Following logging and/or burning, secondary succession enters a grass-forb or weed stage of perhaps 7 years duration. The grass-forb seral stage gives way to a shrub dominated period which in turn is over-topped by tree saplings; generally Douglas-fir.

The composition and density of the seral forest stands are dependent on a variety of environmental factors. Red alder (*Alnus rubra*) stands often develop where disturbance has been great (Newton et al. 1968). A very common occurrence, however, is the development of dense, even-aged stands of Douglas-fir. Such stands frequently are of sufficient density to eliminate understory vegetation until mortality begins to open up the stand. Truly climax forests are rare; old-growth forests, undisturbed for 400-600 years, were once relatively common. Because of the longevity of Douglas-fir, chance occurrence of fires and windstorms historically prevented extensive development of climax western hemlock forests.

In summary, the successional pattern in the Douglas-fir region usually proceeds rapidly through grass-forb and shrub stages to a closed-canopy Douglas-fir forest. When mortality begins to open these stands, western hemlock invades and reestablishment of a characteristic understory takes place. Finally, after 400-600 years without disturbance, a climax western hemlock forest may replace the Douglas-fir.

Succession in Managed Forests

The pattern of succession just outlined is significantly altered when lands are managed for timber in western Oregon and Washington. Fire is widely used for slash removal and seed-bed preparation. Seeding or planting of genetically "superior" stock speeds the reestablishment of preferred timber species, usually Douglas-fir. Herbicide applications, fertilization, and pest control, contribute to the speedy establishment of an even-aged monoculture of Douglas-fir. Stands are thinned periodically and substandard specimens are removed at that time. Harvest occurs at optimal size. Predicted tree age at harvest seems to range from 45 to 140 years depending on site characteristics and the current optimism of the managing agency.

Because of the economic value of timber, managed succession (silviculture) rather than natural succession will be the rule for most of the Douglas-fir region. We identify four areas of concern for forest birds associated with managed succession:

1. Shortening of the grass-forb and shrub stages.
2. Effect of an even-aged Douglas-fir monoculture.
3. Elimination of snags.
4. Elimination of old-growth forest.

AVIFAUNA AND SUCCESSION

Let us now examine the avifauna of the Douglas-fir forests to evaluate the potential impacts of the various modifications of succession. Unfortunately, there have been no quantitative avifaunal studies that follow through the successional stages of the Douglas-fir communities in the Pacific Northwest. What are needed are studies such as those of Johnston and Odum (1956) for the piedmont of Georgia and Haapanen (1965) in Finland. We^{3/} have subjectively placed 84 breeding birds of the Douglas-fir community into five seral stages (Table 1). The assignment to seral stage was our collective estimate based on field experience; we placed some reliance on the habitat descriptions provided in standard northwest bird texts (Gabrielson and Jewett 1940, Marshall 1973, Peterson 1961, Jewett et al. 1953).

The five stages of the Douglas-fir successional series which we recognized are: grass-forbs (1-7 years), shrub-sapling (8-15 years), second growth (16-40 years), older second growth (41-120 years) and mature (over 120 years). The age designations of the seral stages are approximate and subject to variation with site factors and management. Each species was assigned one of three ratings within each stage it was found: X) commonly present, but does not nest; XX) commonly present and nesting; XXX) nesting primarily in that seral stage (Table 1). This rating system indicates how critical a seral stage is to the species. In general, the pattern of species diversity follows that found by other workers (Johnston and Odum 1956, Haapanen 1965): increasing diversity with increasing vegetative complexity.

Note (Table 1) the importance of the second seral stage to the Douglas-fir avifauna. Here some 86 percent of the species use the shrub-sapling stage, and 39 percent nest there. Hole-nesters are represented by only four species.

Our estimates (Table 1) and studies elsewhere (Johnston and Odum 1956, Haapanen 1965) indicate decreased diversity in mid-successional stages (i.e., the 16-40 year-old Douglas-fir second growth). This is related to a reduction in both the complexity and the layering of the vegetation (MacArthur and MacArthur 1961).

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Table 1.--Use by eighty-four birds of Douglas-fir plant communities in Oregon west of the Cascade Mountains summit. Twenty species dependent on holes for nest sites are printed in italics. X = uses that seral stage, but not for nesting; XX = nests in that seral stage; XXX = nests primarily in that seral stage.

Bird species (N = 84)	Serai stage and age, years				
	Grass, forbs, 1-7	Shrub, sapling 8-15	Second growth 16-40	Older 2nd growth 41-120	Mature 120+
Savannah sparrow	XXX	X	-	-	-
Vesper sparrow	XXX	X	-	-	-
White-crowned sparrow	XX	XX	-	-	-
Song sparrow	XX	XX	-	-	-
Nighthawk	XX	XX	X	X	X
Oregon junco	XX	XX	XX	XX	XX
Fox sparrow	X	XXX	-	-	-
Chipping sparrow	X	XXX	-	-	-
Rufous-sided towhee	X	XXX	-	-	-
American goldfinch	X	XXX	-	-	-
Black-headed grosbeak	-	XX	XX	XX	XX
Bewick's wren	X	XXX	-	-	-
Lazuli bunting	X	XXX	-	-	-
Wilson's warbler	-	XXX	-	-	-
Yellow warbler	-	XXX	X	-	-
Nashville warbler	-	XX	XX	X	-
Orange-crowned warbler	-	XX	XX	-	-
Warbling vireo	-	XX	XX	X	X
Solitary vireo	-	XX	XX	XX	-
MacGillivray's warbler	-	XX	XX	XX	XX
Yellow-rumped warbler	-	XX	XX	X	X
Black-throated gray warbler	-	XX	X	XX	XX
Hutton's vireo	-	XX	X	XX	X
Swainson's thrush	X	XX	XX	X	X
Varied thrush	X	XX	XX	XX	XX
Robin	X	XX	XX	XX	X
Common bushtit	-	XXX	X	X	X
Scrub jay	X	XXX	-	-	-
Stellar's jay	X	XX	XX	XX	XX
Western wood pewee	-	XX	X	XX	XX
Western flycatcher	-	XX	XX	X	-
Traill's flycatcher	-	XX	X	-	-
Calliope hummingbird	X	XXX	-	-	-
Mourning dove	X	XX	XX	-	-
Mountain quail	X	XXX	X	X	X
Blue grouse	X	XX	-	XX	XX
Ruffed grouse	X	XX	XX	-	-
Sharp-shinned hawk	-	X	XX	XX	XX
<i>Saw-whet owl</i>	-	X	XX	XX	XX
Cooper's hawk	-	X	XX	XX	-
Pigeon hawk	-	X	XX	XX	-
<i>Pygmy owl</i>	-	X	XX	XX	XX
Long-eared owl	X	X	XX	XX	-
Rufous hummingbird	X	X	XX	XX	XX
<i>Tree swallow</i>	X	XX	XX	X	X
<i>Purple martin</i>	X	XX	XX	X	X
<i>Western bluebird</i>	X	XX	X	-	-
<i>Mountain bluebird</i>	X	XX	X	-	-
Great horned owl	X	X	XX	XX	X
Crow	X	X	XX	XX	XX
<i>Flicker</i>	X	X	X	XX	XX

Table 1.--(continued)

Bird species (N = 84)	Seral stage and age, years				
	Grass, forbs 1-7	Shrub, sapling 8-15	Second growth 16-40	Older 2nd growth 41-120	Mature 120+
Gray jay	-	X	X	XX	XX
Yellow-bellied sapsucker	-	X	XX	XX	XX
Black-capped chickadee	-	X	XX	XX	X
Winter wren	-	X	XX	XX	XX
Golden-crowned kinglet	-	X	XX	XX	XX
Ruby-crowned kinglet	-	X	XX	XX	XX
Red-tailed hawk	X	X		XX	XX
Bald eagle	-	-	-	XX	XX
Osprey	-	-	-	XX	XX
Band-tailed pigeon	X	X	-	XX	XX
Screech owl	-	X	X	XX	XX
Pileated woodpecker	-	-	X	XX	XX
N. three-toed woodpecker	-	-	X	XX	XX
Hairy woodpecker	-	X	X	XX	XX
Downy woodpecker	X	X	-	XX	XX
Olive-sided flycatcher	X	X	-	XX	XX
Chestnut-backed chickadee	-	X	X	XX	XX
Red-breasted nuthatch	-	-	X	XX	XX
White-breasted nuthatch	-	-	X	XX	XX
Brown creeper	-	-	X	XX	XX
Townsend's solitaire	X	X	-	XX	XX
Hermit thrush	-	X	X	XX	XX
Townsend's warbler	-	-	-	XX	XX
Hermit warbler	-	-	X	XX	XX
Hammond's flycatcher	-	X	X	XX	XX
Western tanager	-	X	X	XX	XX
Evening grosbeak	-	X	X	XX	XX
Purple finch	-	X	X	XX	XX
Pine siskin	X	X	X	XX	XX
Red crossbill	-	-	-	XX	XX
Goshawk	-	-	-	X	XXX
Spotted owl	-	-	-	X	XXX
Vaux's swift	X	X	X	X	XXX
SUMMARY:					
Species occurring	38	72	59	64	58
% of total species occurring	45	86	70	76	69
Nesting primarily in that seral stage	2	13	0	0	3
Nesting species	6	39	31	51	46
% total species nesting within seral stage	7	46	37	61	55
Species nesting in holes	0	4	6	14	14

In the fourth and fifth seral stages, fewer total species (64 and 58 vs 72) but more nesting species (51 and 46 vs 39) are present than in the second stage (Table 1). Hole nesting species make up the critical element in this disparity (14 and 14 vs 4).

IMPACT OF FOREST MANAGEMENT ON THE AVIFAUNA

Shortening Period of Early Succession

Manipulation of succession to shorten the length of the grass-forb and shrub-sapling seral stages makes good sense when managing for timber

production. Shortening of this period, however, reduces the duration of relatively bird-rich seral stages (Table 1). At first, most biologists may tend to discount the significance of this effect for several reasons:

a. Forests will be harvested and there will thus always be recycling through these stages. While these stages may be shortened, they will not be eliminated.

b. Timber management seems to be tending toward shorter rotation periods. If a 50-year rotation of Douglas-fir, rather than the 100 year rotation of a few years ago, is realized, there should be twice the area in early succession stages. Overton and Hunt (1974), however, have an alternative view of the yield-rotation question.

Upon closer inspection, however, the choice of methods used to shorten these early successional stages decides the impact of this management scheme on wildlife. Use of herbicides to reduce competition of nonconifers would have drastic impacts on the carrying capacity of the area for wildlife; both numbers and diversity of birds will be markedly reduced.

Management for an Even-Aged Monoculture

The terms "even-aged" and "monoculture" when applied to Douglas-fir forests conjure up in the mind of an ecologist specters of cornfield-like timber stands rich only in their potential for insect outbreaks and mechanized harvest. While these forests of the Pacific Northwest do naturally tend toward even-aged Douglas-fir dominated stands (Franklin and Dyrness 1973), a number of factors disrupt such development. Site factors, animal-caused mortality, and chance occurrences are some primary disruptive sources.

Herbicides or fertilizers may be used to retard or stimulate growth of target species affected by the vagaries of site factors. Berg and Doerksen⁴ indicate that use of both fertilizers and herbicides can be curtailed in some instances. They suggest that foresters may wish to deliberately create red alder understories to fertilize thinned conifer stands. Berg and Doerksen found that a heavy alder understory contributed the nitrogen equivalent of 1,700 lbs of urea per acre over 19 years; and the cost of urea fertilizer has been spiraling. Both trees and birds stand to gain.

Forest managers attempt to manipulate populations of rodents, lagomorphs, ungulates, and even black bears (*Ursus americanus*) to

4/ (In prep.) Natural fertilization of a heavily thinned Douglas-fir stand by understory red alder. Oregon State Univ. For. Res. Lab.

reduce damage to timber. In general, attempts to thwart mammal-caused forest damage have been less than totally successful (Black 1969), and mammals will continue to damage trees and thus unintentionally provide diversity for forest birds.

Insects pose a significant threat to forest yields. Management favoring even-aged, single-species stands essentially sets the table for the insects. We recognize the impact of widespread forest insect outbreaks not only in economic terms but also in terms of forest destruction. Yet, the implications to bird populations of widespread use of pesticides (such as occurred in the northwest with the 1974 DDT-Douglas-fir Tussock moth situation) are a persuasive argument for integrated control as a rational approach to pest problems (Odum 1971:445-447).

Elimination of Snags

Summarizing his research findings in Finnish forests, Haapanen (1965:194) stated that "Taken as a whole, silviculture clearly decreases the densities of bird species nesting in coniferous stands." He further points out that the lower density of hole-nesting birds is the most important factor involved in the decrease of total bird density in managed stands. We have identified some 20 species of hole-nesting birds in the Douglas-fir forests of western Oregon. The requirements of these hole-nesters were reviewed by Jackman (1974a).

Active management of snags for the benefit of wildlife is a relatively recent addition to the forest manager's repertoire in the Pacific Northwest. Gale (1973) investigated types of snags, their densities and use by wildlife in northern California. Bull (1975) calls attention to the selection of large (>58cm dbh), tall (>12m) snags for nesting by pileated woodpeckers (*Dryocopus pileatus*). With these requirements, pileated woodpeckers will be strongly affected by programs which reduce snags in the forest. Studies are now underway at the Oregon Cooperative Wildlife Research Unit, funded by the U. S. Forest Service, to document the demographic parameters of snags in Douglas-fir forests and to quantify their use by wildlife.

Forest managers have responded--preservation of snags for wildlife is rapidly becoming an accepted policy and is being implemented on many northwest forests. As in Finland, (Haapanen 1965), however, the practice of intensive timber management with shortened rotations will eliminate the potential for simple snag preservation to supply the required snags. The time for more creative snag management is here (Jackman 1974b, Bull 1975).

Elimination of Old-growth Forest

There is an element of the avifauna of the Douglas-fir forest that is absolutely dependent on mature forest stands (Table 1). These species have evolved to become specialists requiring the stability and diversity which only old-growth forests can provide. There are, in addition, a whole gamut of species which are dependent to a lesser extent on these old-growth stands. What particularly concerns us is the rate at which old-growth forests, and their attendant wildlife, are being eliminated. The only meaningful stands of old-growth are already limited to public lands.

Over the past several years, one of Wight's students, Eric Forsman, has been studying one of the old-growth obligates, the northern spotted owl (*Strix occidentalis caurina*). In the course of his work, Forsman has located 123 habitats occupied by spotted owls; 64 of these either have been harvested or major harvest is planned. While some may wish to argue over the number of birds remaining, such species surely seem destined for endangered status unless timber management practices are altered.

When all that remains of the mature forest are isolated stands in National Parks and other natural areas, the habitat will become fragmented and exist as scattered islands. The chance for extinction is then a function of population density, habitat size, and the species' ability to disperse and colonize. If this happens, we can take poor solace in the fact that as Bandy and Taber (1974) point out--birds will have it better than other vertebrates.

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Silvicultural Options and Habitat Values in Coniferous Forests¹

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Abstract.--Different bird species select different types and stages of forests which satisfy their requirements for nesting and feeding. Birds are classified into groups based on these requirements (i.e., nests on the ground, feeds on the ground, etc.). The suitability of each bird group for each forest successional stage and the effect on birds of various silvicultural treatments at those stages was judged. The role of birds on insect population control and the effect of fire on bird habitat is examined.

INTRODUCTION

Different species of birds select different types and stages of forest in which to live. There is no argument on this point, and it has been documented by many researchers including Glowacinski (1972), Pitelka (1941), Kricher (1973), Shugart and James (1973), Martin (1960), Odum (1950), Snyder (1950), and Johnston and Odum (1956). The reasons for this selection have been exhaustively reviewed by Von Haartman (1971) and Hilden (1965) and include such variables as food availability, manner of feeding, nesting requirements, physical characteristics, and others. Salt (1953) worked in three coniferous forest types and noted that the nearer the vegetative system moved toward climax the greater the biomass of birds supported. Those species adapted to the more advanced seres had larger body sizes and increased ability to utilize energy efficiently. This was confirmed by Karr (1968) but contradicted by Bock and Lynch (1970).

It has long been recognized that birds respond to environmental features--particularly

vegetative physiognomy (Breckenridge 1956; Lack 1933, 1937; Lack and Venables 1939; Miller 1942; Kendeigh 1947; Klopfer 1965, 1969; Klopfer and Hailman 1965; Svårdson 1949).

Emlen (1956) saw the necessity for describing vegetative habitat characters and suggested rudimentary variables such as canopy height and height to crown, preferring quantitatively to the relative classes described by Kuchler (1949) and Dansereau (1951).

Sturman (1968) expanded this concept to include computed volumes of tree crown to successfully describe habitat selection criteria. Klopfer (1969) and Karr and Roth (1971) noted the importance of canopy layers in accounting for species diversity in forest birds. James (1971) and Cody (1968) dealt with similar thoughts and used discriminate function analysis to describe habitat associations of forest and grassland birds.

MacArthur and associates (MacArthur and MacArthur 1961, MacArthur et al. 1962, MacArthur 1964, MacArthur et al. 1966), developed these concepts to show that the primary variables that could be used to predict species diversity were vegetative volumes by layers and that these layers were essentially three--herbaceous (0-2 feet), shrub (2-25 feet), and tree (>25 feet) layers.

Thomas^{3/} and Thomas et al. (1974) further refined these ideas and showed high correlations of 10 bird species with discrete 5-foot layers of deciduous and conifer vegetation.

^{3/} Jack Ward Thomas. The determination of habitat requirements for birds in suburban areas - a pilot study. Ph.D. dissertation, University of Massachusetts, Amherst. 237 p., 1973.

^{1/} Paper presented at The Symposium on Management of Forest and Range Habitats for Non-game Birds, Tucson, Arizona, May 6-9, 1975.

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Table 1.--Examples of coniferous forest biome bird species typical of each applicable Haapanen's (1965) classification^{1/}

Nests on ground
Feeds on the ground and/or in the air

1. Green-tailed towhee (*Chlorura chlorura*)
2. Oregon junco (*Junco oreganus*)
3. Golden-crowned sparrow
(*Zonotrichia atricapilla*)

Nests on ground
Feeds on bushes and trees

1. Kirtland's warbler (*Dendroica kirtlandii*)
2. Slate-colored junco (*Junco hyemalis*)
3. Spruce grouse (*Canachites canadensis*)

Nests in bushes
Feeds on the ground and/or in the air

1. Townsend's solitaire
(*Myadestes townsendi*)
2. Swainson's thrush (*Hylocichla ustulata*)
3. Varied thrush (*Ixoreus naevius*)

Nests in any kind of bush
Feeds in trees and bushes

1. California thrasher (*Toxostoma redivivum*)
2. Wrentit (*Chamaea fasciata*)
3. Swainson's thrush (*Hylocichla ustulata*)

Nests in coniferous shrubs or seedlings
Feeds on the ground

1. Prairie warbler (*Dendroica discolor*)
2. Black-throated blue warbler
(*Dendroica caerulescens*)
3. Magnolia warbler (*Dendroica magnolia*)

Nests in any kind of tree
Feeds in trees and bushes

1. Olive warbler (*Peucedramus taeniatus*)
2. Ruby-crowned kinglet (*Regulus calendula*)
3. Blackburnian warbler (*Dendroica fusca*)

Nests only in coniferous trees
Feeds in trees and bushes

3. Cape May warbler (*Dendroica tigrina*)

Nests only in spruce
Feeds in trees

3. White-winged crossbill (*Loxia leucoptera*)

Nests in trees
Feeds on the ground or air

1. Cassin's finch (*Carpodacus cassinii*)
2. Sharp-shinned hawk (*Accipiter striatus*)
3. Blackpoll warbler (*Dendroica striata*)

Nests only in very thick branches
Feeds on the ground and/or in the water

1. Western tanager (*Piranga ludoviciana*)
2. Pine siskin (*Spinus pinus*)

Nests in holes, makes a hole, only in hardwoods
Feeds in trees and bushes

1. Acorn woodpecker
(*Melanerpes formicivorus*)

Nests in holes, makes a hole, both hardwoods and pine
Feeds in trees and/or bushes

1. Brown-headed nuthatch (*Sitta pusilla*)
2. Pileated woodpecker (*Dryocopus pileatus*)

Nests in holes, makes a hole, pine or spruce
Feeds in trees and bushes

1. White-headed woodpecker
(*Dendrocopos albobarvatus*)
2. Williamson's sapsucker
(*Sphyrapicus thyroideus*)
3. Black-backed three-toed woodpecker
(*Picoides arcticus*)

Nests in holes made by other species
Feeds in trees and bushes

1. Mexican chickadee (*Parus sclateri*)
2. Black-capped chickadee
(*Parus atricapillus*)
3. Gray-headed chickadee (*Parus cinctus*)

Nests in holes made by other species
Feeds on the ground and/or in the air

1. Flammulated owl (*Otus flammeolus*)
2. Saw-whet owl (*Aegolius acadicus*)
3. Boreal owl (*Aegolius funereus*)

^{1/}

- 1 = Pine zone
- 2 = Fir zone
- 3 = Spruce-hemlock zone

Although we recognize that some bird species have exact requirements in terms of habitat characteristics--such as cavities for hole-nesters (see reviews by Beebe^{4/} and Jackman^{5/} --we proceed from the assumption that silvicultural practices will influence avian habitats primarily through alterations of the form and density of vegetative layers. Further, effects of such alterations can be predicted in terms of their impacts on various classes of birds.

We deal here with principles and generalities due to the magnitude and diversity of the coniferous forests of North America; although throughout the world, conifer forests have been described as inferior to deciduous forests as bird habitat based on bird density and diversity --in Finland: Palmgren (1933), Soveri (1940), Merikallio (1946), Nordström (1953), Jalkanen (1960), Haapanen (1965, 1966), and Portin (1965); in Eastern Europe: Novikov (1962); in Germany: Dirksen and Höner (1963); in the British Isles: Williamson (1969, 1970, 1972); in Australia: Cowley (1971). Urdy (1957) reviewed a number of census efforts in North American forests and reached the same conclusion. Data in Urdy's graphs were interpreted by Von Haartman (1971) in average pairs per square kilometer as follows: deciduous = 719, deciduous-coniferous = 607, and coniferous = 415. Differences are probably related to the relative simplicity--i.e., reduced diversity--in coniferous compared with deciduous forests.

SILVICULTURAL OPTIONS AND BIRD RESPONSES

Silvicultural options that are available to accomplish timber management objectives can have amazingly complex impacts on bird habitats. However, certain basic principles and practices, in one form or another, make up the majority of what we actually encounter. Our discussion is confined to those considerations.

Our typical forest evolves through seral stages of development which we describe as:

bare ground → grass-forb → shrub-sapling
(0-10 years) → poles (11-40) → young
forest (41-100) → mature forest (101-200)
→ old growth (201+).

4/ S. B. Beebe. Relationships between insectivorous hole-nesting birds and forest management. Yale University School of Forestry and Environmental Studies, New Haven, Conn. 49 p., multilithed, 1974.

5/ S. Jackman. Some characteristics of cavity nesters: can we ever leave enough snags? Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis. 10 p., multilithed, 1974.

Haapanen (1965) made a useful categorization of birds based on a combination of nesting and feeding habitat requirements. His life-requirement classification is more useful here than standard classifications based on morphological characteristics. We utilized appropriate portions of Haapanen's system to describe the forest component. We used a simplified version of the coniferous forest life-zones described by Merriam (1894) which may be translated or related to biomes by referring to Odum (1945). As a basis for discussion, we show examples of bird species exhibiting the appropriate characteristics of Haapanen's (1965) descriptive system for the ponderosa pine, fir, and hemlock-spruce life zones (Table 1).

Further, each bird group is best suited to particular stages or combination of stages in forest succession (Table 2). So, natural succession provides a constantly changing series of niches or habitats and their juxtapositions that allow the occurrence of the broad spectrum of species present in the coniferous forest biome (Fig. 1).

Table 2.--Bird species typical of successional stages by life zones in western coniferous forests

Spruce-hemlock zone

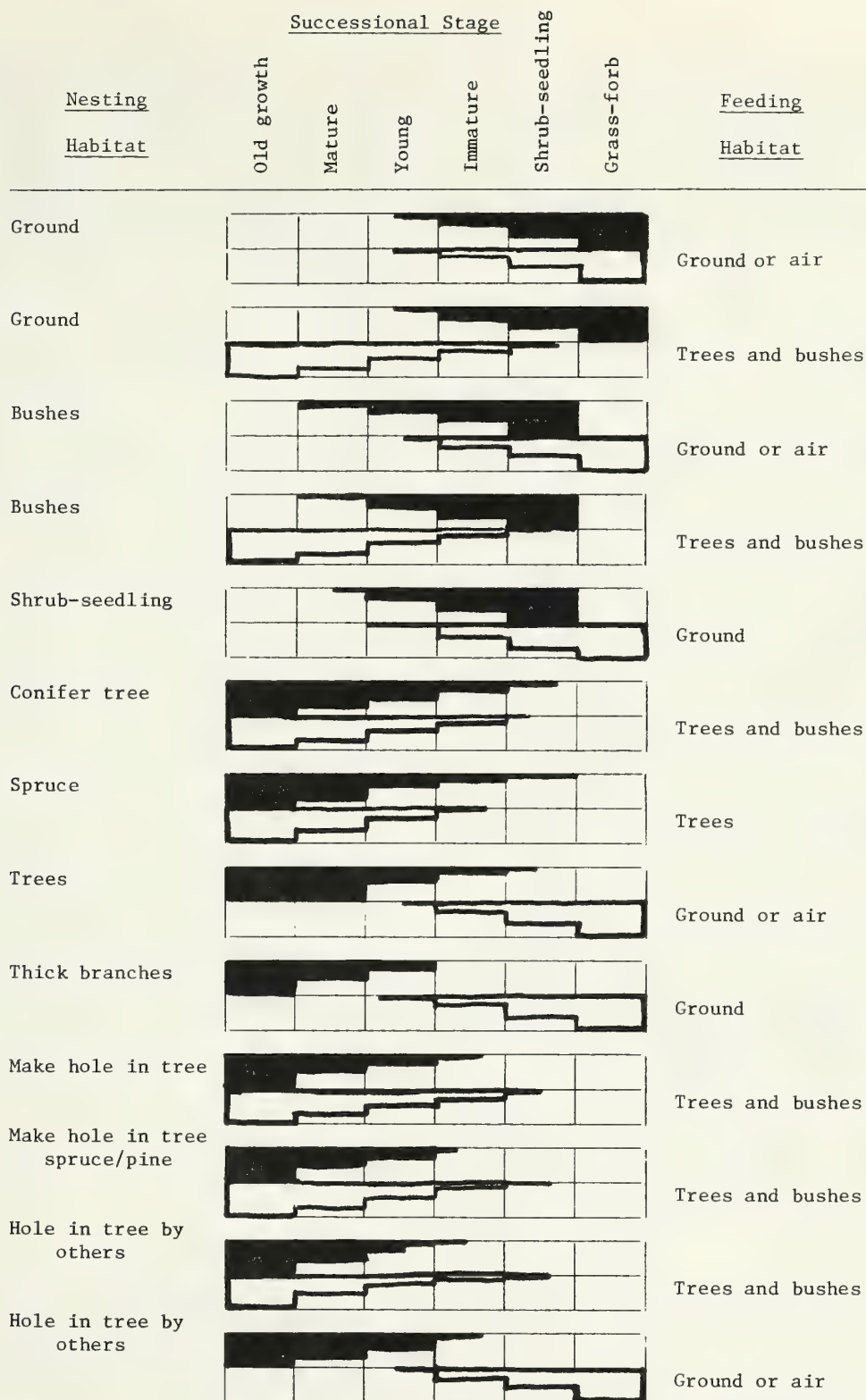
Old growth	Boreal owl (<i>Aegolius funereus</i>)
Mature forest	White-winged crossbill (<i>Loxia leucoptera</i>)
Young forest	Black-backed three-toed woodpecker (<i>Picoides arcticus</i>)
Shrubs	Varied thrush (<i>Ixoreus naevius</i>)
Grass-forb	Golden-crowned sparrow (<i>Zonotrichia atricapilla</i>)

Fir zone

Old growth	Spotted owl (<i>Strix occidentalis</i>)
Mature forest	Pine grosbeak <i>Pinicola enucleator</i>)
Young forest	Williamson's sapsucker (<i>Sphyrapicus thyroideus</i>)
Shrub	Swainson's thrush (<i>Hylocichla ustulata</i>)
Grass-forb	Oregon junco (<i>Junco oreganus</i>)

Pine zone

Old growth	Pileated woodpecker (<i>Dryocopus pileatus</i>)
Mature forest	Red crossbill (<i>Loxia curvirostra</i>)
Young forest	White-headed woodpecker (<i>Dendrocopos albolarvatus</i>)
Shrub	Townsend's solitaire (<i>Myadestes townsendi</i>)
Grass-forb	Green-tailed towhee (<i>Chlorura chlorura</i>)



As the bar width increases, importance increases


 Nesting Habitat  Feeding Habitat

Figure 1.--Suitability of successional stages for bird groups

Table 3.--Bird response to silvicultural treatment^{1/}

Even-aged management

Nests	Ground	Ground	Bushes	Bushes	Coniferous seedling/shrub
Feeds	Ground or air	Tree/bushes	Ground or air	Trees/bushes	Ground

TreatmentOld growth (181+)

Select cut ^{2/}	++	+	+++	+++	+
Clear cut	+	-	++	-	-
Burn understory	+	-	-	---	-

Mature forest (81-180)

Select cut ^{2/}	++	+	+++	+++	+
Clear cut	+	-	+	-	+
Burn understory	+	-	-	---	-

Young forest (41-80)

Select cut ^{2/}	++	+	+++	+++	+++
Clear cut	+	-	+	-	+
Release cut	+++	+++	+++	+++	+++
Burn understory	+	-	+	---	-

Immature (Pole) (11-40)

Clear cut	+	+	+	---	-
Release cut	+++	+++	+++	+++	+++
Burn	+	-	-	---	-

Shrub-seedling (0-10)

Defoliate	+	+	-	-	+
Thin	++	--	--	---	---
Burn	+	-	-	---	--

Grass-forb

Burn	++	+	+	0	+
Plant to trees	-	+	+	++	+

- + Degree of increase benefits for birds
 - Degree of decreased benefits for birds
 0 No effect

^{1/} Bird classification according to Haapanen 1965

^{2/} Includes thinning, salvage and sanitation cuts

Coniferous trees	Spruce	Trees	Thick branches	Make hole pine/hardwood	Make hole pine/spruce	Hole	Hole
Trees/bushes	Trees	Ground or air	Ground	Trees/bushes	Trees/bushes	Trees/bushes	Ground or air
--	---	+	--	+	-	--	-
---	---	-	--	---	---	---	---
-	0	++	++	+	-	-	++
---	---	--	-	+	-	-	-
---	---	---	-	---	---	---	---
-	0	+	++	+	-	-	++
---	---	0	-	+	--	-	-
---	---	--	--	--	---	---	---
+++	+	++	-	++	++	++	++
---	0	+	+	+	+	-	+
---	---	--	--	---	---	---	---
+++	+	+	-	+	+	++	+
---	---	-	--	---	---	---	++
+	+	+	+	-	-	--	++
--	--	-	--	--	--	--	-
-	-	++	++	-	-	--	++
0	0	+	+	0	0	0	++
++	++	+	+	++	++	++	+

Silvicultural treatments are used to alter the natural status of a successional stage to achieve a desired end such as selection for the most economically valued tree species, shortening the time in the "less productive" grass-forb and shrub seres, or concentrating growth on selected stems. In terms of bird habitat, most silvicultural practices can be considered as regeneration of the stand and then, shortening the period between the lower and the most

advanced seres as much as possible.

In the process of "streamlining" the successional process, the application of silvicultural techniques will favor some bird groups and essentially eliminate habitat for others. The consequences of a number of silvicultural treatments at each successional stage are predicted in Table 3.

In general then, the timed harvest of existing forest stands and their subsequent silvicultural treatment until the next generation cut are apt to increase diversity of habitats in the coniferous forest zones, with the result that a greater diversity of species will be encountered in managed forests. This diversity--of habitat and birds--will be subject in several ways to the principle of diminishing returns. In other words, each practice will yield initial large returns in terms of diversity, but each increment will add proportionately less until finally the increments begin to cause losses in diversity.

There is concern that the more intense the forest management system, the simpler the vegetative structure becomes. And, the more simple the vegetative structure, the less diverse the attendant fauna.

So in terms of birds, three primary concerns surface as forest management becomes more intensive; (1) truncated succession, (2) loss of old-growth habitats, and (3) removal of snags or standing dead trees.

Truncated succession is probably important only where grass, forb, and shrub stages are essentially eliminated through programs to return harvested sites to tree cover in the shortest possible time through intensive shrub control and tree planting. Carried to extreme, such practices could have serious impact on those species needing the early successional seres (Table 3 and Fig. 1). Nevertheless, if regeneration cuts are frequent, well distributed, and reasonably small, say 20-100 acres, enough sites should be available in initial successional stages to provide for adequate diversity.

Loss of old-growth forests is much more serious. Wight (1974) discussed the high stability of old-growth conifer forest environments and the extreme specialization of species that are adapted to these environments. He says, "They are doomed if a forest management scheme does not provide for preservation of mature forest habitats on which they are absolutely dependent."

Strong economic pressures always exist to harvest old-growth stands, and it is obvious that present trends for managed forests are leading to shorter rotations. In short, those concerned about birds of the old-growth forests are fearful that, except for specimen or relict stands, the present old growth will disappear by the end of this century. Even those specimen stands will eventually disappear, along with the avifauna that is narrowly adapted to them; and the probability of their replacement

is low (Davis 1974).

If rotation ages are reduced to less than 100-150 years, a much larger component of the avifauna will be threatened by destruction of their nesting habitat. These are the cavity nesters, and the dead trees (snags) of sufficient sizes to meet the needs of some species are products of older age classes of trees. In conifer forests, some 20 percent of total breeding pairs nest in holes (see footnote 5).

Intensive forest management presents a double threat to availability of snags: (1) the loss of existent snags due to safety requirements imposed by State and Federal regulations and (2) lack of replacement snags during shorter rotations and continued removal of potential snags during thinnings. Safety regulations presently require that virtually all snags adjacent to haul or skid roads, in or near landings and work area, be felled, which indicates that few or no snags will remain at rotation. Shorter rotations may be even more devastating in the long run, and the only solution may be to program some stands or individual trees in each management unit for long rotations to provide continuous supply of snags. Potential snags should be as carefully husbanded as selected crop trees for they will provide tomorrow's crop of hole-nesting birds. Haapanen (1965) noted that bird species diversity was less in managed than unmanaged Finnish forests and attributed the difference to loss of suitable sites for hole-nesting birds under management. Similar observations concerning deciduous forests in Michigan were noted by Gysel (1961).

In summary, and considering only birds, it seems to us that present trends in timber management will lead to diversity that will be generally reflected in increased diversity of bird species as outlined by Hagar (1960). The exceptions will be those species adapted to old growth and those requiring snags for nesting. Pengelly (1972) presents a more pessimistic view concerning effects of intensive forestry on wildlife in general. Counter arguments are presented by Hoooven (1973).

BIRDS AND INSECT CONTROL

There are two sides to this topic--what roles do insect-eating birds play in the control of insect populations and, conversely, what effect does the control of insect outbreaks through use of pesticides have on populations of insect-eating birds? We will address only the first of these.

The questions have been extensively reviewed by the German workers (Bruns (1960), Franz (1961),

and Herberg (1965). Beebe (see footnote 4) thoroughly reviewed relationships between insectivorous hole-nesting birds and forest management, including the bird/insect interface. Buckner (1966, 1970) addressed the role of vertebrate predators in insect control.

The questions should also be put in an economic perspective by enumerating the costs of forest insect outbreaks--both in direct losses and in costs of control programs and rehabilitation efforts. For example, some \$12,000,000 was spent annually over the period 1960-70 to control epidemic insect outbreaks in the western United States alone (USDA Forest Service 1973). A more revealing examination of the complex costs of a recent outbreak is shown in the environmental impact statement prepared for the request to use DDT to control an outbreak of the Douglas-fir tussock moth in Oregon, Washington, and Idaho (USDA Forest Service 1973).

Early workers (Beal 1906, 1911; Forbush 1907; McAtee 1911, 1915, 1926; and others) vividly documented the astounding numbers of insects that are consumed by birds. They had a tendency perhaps to overstate the case. For example, McAtee (1926) refers to many instances of control or suppression of insect populations by birds alone. Later detailed work on the myriad of factors bearing on insect levels in forests casts some doubt on such simplistic interpretations (Tinbergen 1960, Morris 1963). In fact, Tinbergen (1960) contended that the exact relationship of birds to insect population dynamics could be shown only by intensive study of a single bird species over a large area for a prolonged period. Popelov (1956; quoted in Otvos 1965) expanded that restriction to indicate that the determination must be made for each bird species, insect species, and forest stand. Beebe (see footnote 4) listed a number of studies indicating that birds help regulate spruce budworm populations at endemic levels (Kendeigh 1947, Morris et al. 1958, Morris 1963, Dowden and Carolin 1950, Dowden et al. 1953, George and Mitchell 1948). Similar relationships have been described for the larch sawfly in isolated stands (Buckner and Turnock 1965); woodpeckers and western pine beetle (Otvos 1965); woodpeckers and other beetles (Massey and Wygant 1973); and tits on moth larvae (Gibbs 1958, 1959).

Beebe, p. 27-28 (see footnote 4), says that--

With few exceptions the conclusions of literally hundreds of papers dealing with the impact of avian predators on their insect prey have been that, in many instances, birds act as

important components of natural biological regulation of insect population dynamics at endemic... levels. In...unusual circumstances birds may act together, each species and sometimes each sex in its own specialized way, to be a major cause of the suppression of an insect outbreak...the most important role of birds is in the prevention of insect epidemics, rather than their suppression. This important role is probably still underestimated because the vast majority of research has been conducted during insect epidemics in which the sheer numbers of insects simply overwhelm the birds' ability to exert regulatory influence.

Beebe, p. 19 (see footnote 4), also cautioned that findings presented in his extensive literature review "must be qualified by the understanding that our knowledge of the relationships between insectivorous birds and their prey is very limited."

There are instances where birds might have reduced epidemic populations of insects. Woodpeckers seemingly had such an effect on outbreak populations of southern hardwood borers (Solomon 1969, 1970). Knight (1958) and McCambridge and Knight (1972) also reported control of Engelmann spruce beetle by woodpeckers.

Benefits have also been reported from large numbers of birds "drifting into" or aggregating in areas of outbreak during the winter. This phenomenon has been most frequently noted in woodpeckers of various species (Blackford 1955, Koplin 1969, Baldwin 1960) but has also been reported in many other species and groups (Turcek 1949, Blais and Parks 1964, Sloan and Coppel 1968, Coppel and Sloan 1970, Mattson et al. 1968, Dahlsten and Herman 1965). The importance of birds as a biological control mechanism has received more detailed attention in Europe where shorter rotations, intensive forestry, and loss of snag habitats have been evident for much longer than in North America.

The literature reviews by Poznanin (1956), Bruns (1960), Franz (1961), and Herberg (1965) cover this topic. For example, Franz (1961) cites 229 references to support his conclusion that birds, along with insectivorous bats, small mammals, microbials, and predatory insects, help hold insect populations at endemic levels or exert some control at early outbreak stages. Bruns (1960) cites papers reporting that satisfactory control of insect populations by hole-nesting birds was increased by installing nest

boxes (von Berlepsch 1926, Appel and Schwartz 1921, Freiburger 1926-27, Hähle 1946, Herberg 1965).

The importance that European forest land managers place on insectivorous birds as biological control agents is reflected in the funds expended to provide artificial nesting cavities for these species. In addition to literature already mentioned, Cole (n.d.) noted that installation of boxes is common in Bavarian forests and that some 400,000 boxes have been placed over an area of 140,000 hectares and another 300,000 are planned in Spain (Molina 1971).

Bruns (1960, p. 204) provides an apt conclusion for this section:

Birds are not a complete remedy. On the balance of opinions and considering recent investigations, the truth may lie neither in the one, nor in the other direction, but in between. I mean to say that, within the community of all animals and plants of the forest, birds form an important factor. The birds generally are not able to break down an insect plague, but their function lies in preventing insect plagues. It is our duty to preserve birds from (sic) aesthetic as well as economic reasons, and to create artificial compensation in the form of nest boxes, where nesting chances are diminished by the forestry work....The wood is still able to defend itself biologically against insect plagues. It is our duty to conserve these biological forces (birds, bats, wood ants, parasites) and to conserve or create a rich and diverse community. By such a prophylactic, carrying out of "hygiene" before a possible outbreak of an insect pest, the forests will be better protected than by any other means. If there should be further insect plagues their effect will at least be diminished, so that we will only need to use chemical control in exceptional circumstances.

FOREST BIRDS AND FIRE

Most published work concentrates on responses of gallinaceous birds to fire, and the use of fire to produce suitable habitat

for nesting, feeding, and hiding for these birds. The pioneering research has been carried out under the auspices of The Cooperative Quail Study Association whose efforts and numerous publications are summarized in the Tall Timbers Research Station (1961). Most notable among these contributions was that of Stoddard (1931) on bobwhite quail. Sharp (1971), Bump et al. (1947), Grange (1948), Vogl (1967), Wheeler (1948), Stoddard (1935, 1961), Doerr et al. (1971), Ligon (1946), and others have discussed the effects of fire on ruffed grouse populations.

Responses of non-game birds to wildlife or controlled burning have received considerably less attention. The role that fire may take in the creation of desired wildlife habitat has been discussed by Komarek (1966) and Neel (1967). The generalized theory that fire can be used to open clogged understory, remove rank vegetation, set back plant succession, stimulate plant growth, and improve nutritional status of forage thereby creating the diversity and conditions suitable for desired forms of wildlife was considered by Komarek (1963), Miller (1963), and Stoddard (1963).

Actual studies of the relationships of fire and non-hunted bird species are rare. Marshall (1963) related the difference in the avifauna of a mixed pine-hardwood forest subject to frequent fires to one where fire was excluded. Repeated understory fires had produced park-like forests compared with stunted, tangled stands where fire had been excluded. The birds present in each area reflected these habitat conditions. Species adjusted to open understory and scattered trees were abundant in the burned area, whereas those that preferred a heavy shrub layer and/or crowded woods were more common in the woodland where fire was excluded. Komarek (1969) reviewed the literature concerning fire and animal behavior as well as listing positive reactions of 77 bird species to burning or burned areas. He concluded that many animals are adapted to a fire environment and natural selection has been a major factor in such adaptation.

Bock and Lynch (1970) studied the breeding bird populations on burned and unburned areas in the Sierra Nevada. They found a dramatic difference in numbers of birds classified as "tree foliage-searching," which represented 47.9 percent of the birds in the unburned area and 8.7 percent in the burned area, and the "ground-brush foraging," which amounted to 29.4 percent in the unburned and 60.9 percent in the burned area. The total numbers of birds were virtually the same between treatments, but biomass on the burned plot was markedly greater.

Kilgore (1971) studied the effects on the avifauna of removal of the sapling and brush layer of a giant sequoia forest by various means including controlled burning. Opening the lower layer produced changes in species composition but not in biomass. Understory thickets were apparently less useful than canopy and trunk components for nesting and feeding. Three species of ground nesting and/or feeding birds were eliminated while flycatchers and robins increased in numbers.

Emlen (1970) described bird response to a controlled burn of a 400-hectare block of 20-year-old slash pine in Florida. This fire caused a drastic reduction of ground cover and shrub foliage. The overstory was essentially unchanged. Bird counts were made on the burn and in adjacent unburned stands. The avifauna was expected to reflect changes in the vegetative physiognomy but did not, suggesting that food and shelter resources were not equally disrupted by the fire. The attachment of resident species to established home ranges and foraging territories could have explained the lack of response as the only two species showing measurable reactions were spring migrants to the area.

Mayfield (1960) determined that Kirtland's warbler was the product of a particular sere in jackpine communities that is produced by periodic burning. A concerted management effort is underway by the U.S. Forest Service to maintain the habitat of this rare species through periodic controlled burns.

Lawrence's (1966) work with chaparral fires in the Sierra Nevada foothills indicated that an increase in bird species diversity could be expected following fire due to the increased diversity of the environment caused by reduction of brush and the increases of grass and forbs. Avian predators concentrated in the burned areas to take advantage of the increased vulnerability of rodents.

It seems likely that the avifauna may react similarly to either fire or mechanical techniques that reduce or retard succession. This opinion is based on the premise that most bird species react primarily to the physiognomy of the vegetation (Hilden 1965, MacArthur and MacArthur 1961, MacArthur et al. 1962, Thomas et al. 1974; also see footnote 3).

Fire effects on the total forest ecosystem is discussed by Biswell (1967), Thompson and Smith (1971), and others who point out the role of naturally occurring fires and those set by the aboriginal North Americans in the evolution and development of forests. Essentially, fire exclusion leads to overstocked

stands, stagnant stands, cluttered understory, accumulation of organic material at ground level, invasion of fire-susceptible species and loss of diversity in forest plant systems. In addition, the probability of catastrophic fires is increased.

Regarding the avifauna, we suggest that this is neither good nor bad--it merely is. The avifauna changes to include those species best adapted to, and most favored by, a new habitat complex. The thing to recognize is that burning, controlled or wild, will probably add diversity to a forest and cause changes in the avifauna that reflect habitat alterations.

CONCLUSIONS

The coniferous forest moves through successional stages from bare ground to old-growth stands. Each stage in succession is more or less favorable to each bird group in terms of habitat requirements, and therefore, there is a successional pattern in the avifauna reflecting changes in the forest vegetation.

Silvicultural treatments have the general effect of modifying successional patterns to achieve some timber-related objective to speed up succession, to select for certain plant species, to concentrate growth on selected stems, or to harvest valuable commodities. The effects of such silvicultural options are predictable and controllable.

Birds are a natural part of the coniferous forest biome. They evolved with it and influence the system as well as being influenced by it. The effects of birds in the population dynamics of forest insects is one role that we have discussed.

Applied fire management is just coming into its own. Fire can be used for several purposes--but primarily results in alteration of ground cover or successional patterns.

Opportunities for wildlife biologists to attain their forest management goals were never better. Many, if not most foresters are now receptive to reasonable proposals to enhance bird habitats or at least to minimize adverse impacts of silvicultural practices on the habitats. However, biologists must provide factual, professional, and realistic leadership in planning and implementing land management policies and programs if habitat diversity and attendant bird species diversity are to be maintained.

Finally, land managers who can't see the ecosystem for the trees are in for hard times because effects of silvicultural practices reach far beyond the care and feeding of trees. Their work will be judged not only in terms of meeting timber production goals, but in how well their management decisions protect and enhance all components of forest ecosystems including the forest-dwelling birds.

As is often the case, Aldo Leopold (1962, p. 68) said it best:

I have read many definitions of what is a conservationist and written not a few myself, but I suspect that the best one is written not with a pen but with an axe. It is a matter of what a man thinks about while chopping, or while deciding what to chop. A conservationist is one who is humbly aware that with each stroke he is writing his signature on the face of his land. Signatures of course, differ; whether written with axe or pen, and this is as it should be.

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Watershed Management Practices and Habitat Values in Coniferous Forests¹

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Abstract.--Application of watershed management practices in coniferous forests can produce thinned stands, cleared openings, and new plantations. Clearcutting patches to increase water yields has the greatest potential for changing nongame bird habitats. Changes in the vegetative cover will increase habitat diversity, which is frequently, but not always, beneficial to birds.

Watershed management practices in coniferous forests and plantations are applied to:

1. Increase the amount of water available for domestic use and irrigation.
2. Reduce the amount of sediment carried to streams, lakes, and reservoirs.
3. Reduce peak flows to lessen the danger of flooding.

We will describe how vegetation is modified to attain each objective, and the reasons why certain treatments are necessary. Then we will examine these modifications in relation to possible changes in nongame bird habitats.

The second and third practices listed have less potential than the first for changing nongame bird habitats. The areas treated are relatively small and often represent departures from natural habitats even before treatment. Emphasis, therefore, will be on the reasons for and the probable effects of practices intended to increase water yields from conifer-covered watersheds. Such treatments can radically change existing coniferous stands, and may someday be the most important watershed management activity in terms of the number of acres

involved. The other practices, however, do produce valuable responses and will not be ignored.

INCREASING WATER YIELDS

Water yields are increased by diverting a greater percentage of total precipitation to streamflow and reservoir storage. This is accomplished primarily by reducing:

- (1) interception of rain and snow by vegetation,
- (2) evaporation of water from snowpacks and vegetation, and
- (3) transpiration of water by vegetation.

Each of the items listed contains a reference to vegetation. Moisture losses are reduced by modifying the vegetative cover.

Three climatic conditions determine the practices used to increase water yields from coniferous forests:

1. Some conifers grow where most or all of the annual precipitation falls as rain. Such forests occur in the Southeastern States and at lower elevations along the Pacific Coast. The latter region has the highest annual precipitation of any area of the United States.
2. Snowmelt and rainfall are both important sources of runoff in the coniferous forests of the Northeast. Together they produce heavy spring runoff. Rainfall during the rest of the year produces about half the annual

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streamflow.

3. Other coniferous forests are in regions where snowmelt is the source of most of the water produced by the watersheds. Areas fitting this third situation are the mountains and high plateaus of the West. There is great interest here in practices that can increase water yields. These forests are on the headwaters of major rivers that flow through regions where local precipitation is much less than domestic, industrial, and agricultural needs.

Since there are some differences in the hydrologic processes involved, snowpack management and rainfall management are described separately.

Rainfall Management

Water yields can be increased by reducing interception and transpiration losses in regions where rainfall is a major contributor to streamflow. Part of every storm soaks the trees and then evaporates back to the air. A large percentage of the total rainfall of each small storm leaves the watershed this way, especially in areas of dry climate. Interception by pines in South Carolina (Swank 1968) and Douglas-firs in Oregon (Rothacher 1963) amounts to about one-fifth of total annual rainfall.

Transpiration by trees removes large amounts of the rainfall that reaches the ground and accumulates as soil moisture. This transpiration continually produces a deficit in soil storage that is satisfied by diverting part of the rainfall of subsequent storms that would otherwise go to streamflow.

Clearcutting part or all of a watershed can increase water yields where rainfall is an important part of total precipitation. With seasonally variable precipitation, most of the increase will appear during the rainy season. Increased yield from a watershed will approximately conform to the proportion of watershed area that is cleared (Rothacher 1970). There is a high potential for yield increases in the southern pine and northeastern conifer regions (Lull and Reinhart 1967). An increase of 18 inches annually was measured on the clearcut parts of a Douglas-fir forest in the high precipitation zone of Oregon (Rothacher 1970).

Snowpack Management

The sequence of events necessary for an increase in water yield from snowpacks indicates the type of cutting needed for success. The sequence is as follows:

1. Clearing blocks, patches, or strips of trees changes the pattern of wind movement across the forest canopy, and thus changes the pattern of snow deposition on the ground (Anderson 1963). Snow accumulation is greater in openings than in the adjacent forest (Gary 1974). Total snow storage on the watershed, however, is not changed by the cutting (Anderson and Gleason 1959, Hoover and Leaf 1967).
2. Snow melts faster in openings than in the forest during the spring melt period (Bates and Henry 1928, Gary 1974, Leaf 1974). A smaller percentage of the water content of the snowpack is lost to evaporation than with a slower melt rate.
3. In cleared areas, less water is needed to recharge the soil to maximum water-holding capacity. Soil moisture at the beginning of the melt period will already be higher in clearings than under adjacent forest because transpiration and interception by trees has been eliminated (Dietrich and Meiman 1974, Herring 1970, Orr 1968). Also, there will be no losses to transpiration by trees during the melt period.
4. Fast melting of a large snow accumulation with less diverted to evaporation and soil moisture and none used in transpiration by trees results in more water moving toward stream channels. Most of the annual increase in water yield will accrue during the spring melt period.

For the subalpine forests of Colorado, it has been suggested that this sequence could be generated by converting about 40 percent of a watershed to openings. The patches should be about 5 to 8 tree heights in width and about 5 to 8 heights apart (Hoover 1969). To preserve scenic values, the openings should be arranged to fit the landscape. Patch cuttings are consistent with silvicultural considerations, since increases in water yields may not be reduced until the replacement trees are 30 years old. Treatment effects may not disappear completely until the new crop is 60 years old (Leaf 1974). The effective period is long because of the relatively slow growth of subalpine trees.

Increased water yield after clearing patches, strips, or larger areas has been measured on gaged watersheds in several coniferous types. Increases have been found across the West from the mixed conifer (Rich 1965) and ponderosa pine (Brown et al. 1974, Rich 1972) of Arizona, to the subalpine forests of Colorado (Bates and Henry 1928, Martinelli

1964), and the ponderosa pine of Idaho (Haupt 1951).

Recommendations on width of cleared areas range from 1/2 to 8 tree heights, varying between and within forest types. A width of opening about 4 times the height of the adjacent trees at rotation age is perhaps an average of published values. The objective is to have an opening large enough to change the windflow and snow deposition patterns, and be at least partially free of live tree roots. Openings should not be so large that water will be lost from the snowpack before the spring melt period.

Selective cuttings or thinnings do not materially increase water yields unless reserve tree densities are very low (Brown et al. 1974, Rich 1965, Rich and Thompson 1974). Interrupting the forest canopy sometimes causes more snow to be deposited in the partially cut areas. Without extreme reductions of trees, however, much of the soil remains occupied by the roots of living trees. Moisture that might otherwise be in excess of losses produces an increase in growth of the remaining trees and cannot appear as increased yield. This is the response sought when thinnings are made in forest stands to benefit wood production.

REDUCING SEDIMENTATION

Soil erosion and the resulting sediment carried to streams and lakes can be reduced by planting trees on abandoned farms and other disturbed areas (McClurkin 1967). Stabilization of the soil preserves the soil resource, reduces the cost of treating domestic water supplies, prolongs the useful life of reservoirs, and maintains good habitat conditions for aquatic species.

Conifer plantations, especially pines, have been widely used for erosion control (Ursic 1963). The trees produce a litter layer at the soil surface and organic matter in the upper soil layers. These encourage rapid infiltration of water into the soil mantle and reduction or elimination of surface runoff. With little or no overland flow, there is no force to create sheet or gully erosion. A litter layer also prevents splash erosion from falling rain. Conifers have also been planted around municipal reservoirs to keep hardwood leaves, and resulting discoloration, out of the water (Lull and Reinhart 1967).

Effectiveness of conifer plantations in combating soil erosion varies by region. Plantations are highly effective in the Southeast where high rainfall encourages high survival and growth of the transplants. Planting

is much less useful in the semi-arid forest regions of the West. The erosion potential is much greater, and low survival and slow growth of the trees delay the healing process.

Replacement of grasses or hardwoods with conifers may increase interception and transpiration losses and reduce the amount of usable water produced by a watershed (Ayer 1968, Hill 1960, Swank and Douglass 1974). The adverse effect of a plantation on water yield increases as the trees become older and larger (Eschner and Satterlund 1966). This side effect can be important, considering the popularity of pine plantations for stabilization of municipal watersheds in the eastern United States.

REDUCING PEAK FLOWS

Reduction of peak flows to reduce the danger of flooding requires lengthening of the period in which water moves to stream channels (Connaughton 1935, Hoover 1960). As with erosion control, it is necessary to maintain good infiltration conditions at the soil surface. Water then moves into the soil mantle, at least temporarily, instead of flowing rapidly across the soil surface, as is usual in disturbed areas. Conifers can provide the litter and humus needed to maintain adequate infiltration rates. During the growing season, soil moisture is reduced through transpiration and interception (Schneider and Ayer 1961). This can provide temporary storage space for water except where rain falls frequently and the soils are continually wet.

Conifers can be used to reduce peak flows in two ways. Existing stands should be cut only by light partial removals, so that water yields are not increased. Plantations should be established on disturbed areas if enough area can be planted to influence an entire small watershed (Ayer 1968). Potential for benefits is high in the Southeast. Little can be accomplished in the Northeast because individual ownerships are too small in most areas to beneficially affect watershed behavior. Unfortunately, no forest condition can provide protection against high-intensity storms or against lesser storms if little soil-moisture detention storage is available.

Maintenance of shade over the snowpack may be appropriate if much of the annual runoff comes from snow. This sometimes prolongs the period of melt to prevent sudden buildup of spring runoff. Adequate shading can be provided in forest stands by selective cutting or by cutting strips narrow enough to be shaded by adjacent uncut trees. Melting of snowpacks

in brushfields may be delayed by replacement of the brush with coniferous trees (Anderson 1963).

EFFECTS ON BIRD HABITAT

References cited in the previous sections indicate that watershed management practices with conifers can involve:

1. Cutting numerous patches or strips, each several acres in size.
2. Thinning stands to very low reserve densities.
3. Establishing plantations of coniferous species.

Each of these will change existing habitat conditions, including the degree of plant diversity. Only a few studies of birds have been made in conjunction with application of watershed management practices. It is necessary, therefore, to also search reports describing other situations to determine the probable effects of the treatments on nongame birds.

Patch or strip cutting will create additional acres of grasses, shrubs, and small trees; increase the length of edges between dissimilar vegetative types; change the relative amounts of the various kinds of bird food produced; and reduce the area of continuous mature forest. No general statement can be made concerning the desirability of these changes for nongame birds. The requirements of each species or group of species and the area of each tract modified must be considered individually.

Alternate strip cuttings 1 to 6 chains wide that covered 40 percent of the Fool Creek watershed in Colorado (Martinelli 1964) appear to be attractive to some birds. More than a dozen species feed in the openings and nest in trees at the edge of the uncut strips. Visual and sound observations of birds are frequent. In contrast, the dense subalpine forest on an adjacent, undisturbed watershed provides only an occasional sound from a woodpecker.

Some indication of the effects of patch cuttings on birds has been obtained from observations of burned areas. The burned areas studied, however, were much larger than patches created to increase water yields. In a lodgepole pine forest, the number of species and breeding pairs in burned areas increased with years since burning, until the canopy of the new pine stand closed. Crown closure occurred when the young trees were more than 25 years old. In contrast, 300-year-old stands with a sparse understory were much less used by birds (Taylor 1973). A plot on a large burn in the Sierra Nevada had only a few more breeding

birds than a plot in unburned mixed conifer forest with a well-developed understory. Total avian biomass, however, was much greater on the burned plot because birds characteristic of the openings averaged heavier than forest dwellers (Bock and Lynch 1970).

Enthusiasm for increasing habitat diversity sometimes must be tempered with caution. For example, the spotted owl, a threatened species, occurs in western coniferous forests that are important water producers. Each pair of this extremely sedentary species requires 300 to 600 acres of dense, old forest (Zarn 1974). Creating the numerous patches of several acres each that are needed for a significant increase in water yields can make an entire watershed unattractive to this rare species. Zarn (1974) suggested several restrictions on human activity for areas where spotted owls are known to occur. Two restrictions pertinent to patch cutting were: (1) no cutting along the permanent water course closest to the nest area, and (2) protected areas should include the entire hillside from drainage area to ridge top. Spotted owls are so rare and so strongly restricted to forests below the subalpine zone that they do not occur in most of the coniferous area of the West. This rarity requires that land managers give them every consideration where they do occur.

Thinning coniferous stands to very low densities greatly changes habitat conditions. Thinned areas are unattractive to birds that require closed forest, such as the spotted owl, and to those that need fully open, herbaceous communities. Thinned stands, however, do provide great variety on a single acre. Trees are still available for feeding and nesting, and the food produced by herbaceous plants and shrubs increases in proportion to the degree of thinning.

Heavily thinned areas can be attractive to some species of birds. Screech owls prefer to hunt among widely spaced trees over a grassy ground cover (Scott and Patton 1975). Heavy thinning on one of the Beaver Creek experimental watersheds in Arizona was followed by a great influx of Lewis' woodpeckers.

Thinning for increased water yield, like silvicultural thinnings, can have adverse impact on some birds. An extreme case is the red-cockaded woodpecker, an endangered species. Although these woodpeckers do not seem to be affected by variations in stand density, the older trees with heart rot that are essential for nesting are the ones most likely to be removed for silvicultural reasons (Lay and Russell 1970, Ligon 1970). In this and similar cases, the goal of forest practices should be something other than perfect silviculture. We have handled this problem on the Manitou

Experimental Forest in Colorado by tagging live and dead nesting trees with metal warning signs before marking for cutting begins (Myers 1974).

The value of soil conservation plantings to wildlife has been demonstrated throughout the United States. Conifer stands are especially attractive to birds when they are open enough to permit vigorous growth of understory shrubs. Such plantations, however, will displace species such as horned larks that prefer more open habitats (Hawbecker and Bond 1942). The degree to which this is harmful will depend on the availability of alternate open spaces not already occupied to capacity. The influence of a plantation will also depend on its degree of isolation from other coniferous areas. It is possible that some suitable stands will not be found by bird species that can use them.

The interiors of large conifer plantations old enough for the tree crowns to close are unattractive to many species of birds. Plantations should not be larger than 7 to 8 acres where wildlife is an important consideration (Bailey and Alexander 1960).

Plantations of the southern pines for watershed management objectives could play an important part in preservation of the red-cockaded woodpecker. Trees more than 75 years old are used for nesting because they are most likely to have portions softened by heart rot that can be excavated for nest cavities (Lay and Russell 1970). Wood production areas have few trees 75 years old, even where sawlogs are produced. Some plantings for soil stabilization will not be under similar economic pressure, and perhaps could be left to reach ages where they will be attractive to this rare woodpecker.

RESEARCH NEEDS

Watershed management practices designed to significantly increase water yields will produce great changes in the landscape in terms of both plant and bird communities. We need to be able to predict the effects of these changes so the land manager can make sound decisions before treatments are applied.

A competent birder can accurately predict the bird species to be found in a relatively homogeneous plant community. His accuracy may diminish considerably, however, in habitats of complex vegetational structure. Much progress has been made in defining the relationships between habitat structure and bird populations in simple habitats (MacArthur et al. 1962). Our knowledge about complex habitats is rather limited, however (MacArthur 1964). Since current watershed management practices will tend to produce patchy--and thus complex--

habitats, research on the effects of these practices on bird populations is of high priority.

How size and shape of timber cuts, the pattern of these cuts on the watershed, and the size of the treated area in relation to adjacent areas, affect bird populations are practically unknown. These relations need to be quantified for the land manager who, all too often, must make an intuitive judgment in the balance of economic development and wildlife values.

A suitable approach for research appears to fall in the following sequence:

1. Establish basic census standards and criteria for evaluating effects of watershed management practices on bird populations.
2. Determine the habitat variables that affect bird populations and formulate prediction tools.
3. Test these tools on large-scale watershed operations.

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Spotted owl (Strix occidentalis). USDI
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Scientific Names

Trees

Douglas-fir	<u>Pseudotsuga menziesii</u> (Beissn.) Franco
Lodgepole pine	<u>Pinus contorta</u> Dougl.
Ponderosa pine	<u>Pinus ponderosa</u> Laws.

Birds

Horned lark	<u>Eremophila alpestris</u> (Linnaeus)
Lewis' woodpecker	<u>Asyndesmus lewis</u> (Gray)
Red-cockaded woodpecker	<u>Dendrocopos borealis</u> (Vieillot)
Screech owl	<u>Otus asio</u> (Linnaeus)
Spotted owl	<u>Strix occidentalis</u> (Xántus)

Discussion

MR. EVENDEN: The last several days we have heard a number of people say that we really aren't able to get into management of nongame types because we don't know enough. Dr. Thomas, how does this fit with what you said in your opening remarks as to the urgency of the situation?

DR. THOMAS: I do not think of any of us in the room are satisfied. But conversely, we know a whole lot. We know enough to failsafe on say 95 percent of the species. For the other 5 percent we're on thin ice. We must have additional specific information on those.

MR. NEWMAN: Dr. Wiens, I would like to have you elaborate a bit on your comment: "Our objectives should be not to manage for diversity, rather to manage for natural communities."

DR. WIENS: I think by natural communities

what one really has in mind are communities that are characterized by species assemblages which are normally found in relatively undisturbed successional stages rather than species assemblages which show obvious artificiality.

MR. BEALER: Dr. Wiens, you reached a tentative conclusion that the warblers were not controlling insect outbreaks. Do you have some idea on what the controlling factors were?

DR. WIENS: I think the body of evidence that has been amassed by forest entomologists indicates that in many epidemic situations there is effectively no control. An insect runs out of food.

DR. THOMAS: The most important role of birds is prevention of epidemics, rather than suppression.

Thursday Afternoon, May 8

**Management of Nongame Birds in
Current Policies and Decision Making**

*Moderator: W. L. Pengelly
University of Montana*



Management of Nongame Birds in Current Policies and Decision Making: Industrial Forests¹

Carroll J. Perkins^{2/}

The policies of the various companies within the forest industry and how these policies are formulated are subjects that do not lend themselves readily to scientific research. All too often the forest industry is considered as an entity with a uniform belief, policy, and modus operandi. The truth of the matter is that the forest industry is made up of as many beliefs, policies, and actions as there are companies in it. Undoubtedly, there are as many companies as there are species of songbirds, and their policies are as diversified as are the habitat requirements of the various avian species. For this reason, we should not attempt to lump the overall "Policy of Industry" into one category, no more than we should speak of a "Songbird Habitat" as though it accommodated all species of birds.

In the preparation of this paper my first inclination was to conduct a survey among the leading forest industry companies. However, after consideration, I concluded that many of the questionnaires would be answered by overly enthusiastic public relations personnel offering information that would be of little scientific significance. Therefore, the information in this paper will not be scientific in nature, but will be derived from 16 years of my personal observation and experience while working with forest industry in the South.

The first impact the forest industry had on wildlife in southeastern United States began around the turn of this century. Vast stands of virgin timber were harvested at that time with little or no regard for the effect on wildlife. The destruction of wildlife habitat; the rise in human populations and, subsequently, the number of hunters; the improvement in the quality of firearms and ammunition; and the increased accessibility of these areas, often contributed to the elimination of many species of wildlife, particularly those with a low reproductive potential. Black bear (*Euarctos americanus*), Red wolf (*Canis rufus*), Cougar

(*Felis concolor*), American beaver, *Castor canadensis*, White-tailed deer (*Odocoileus virginiana*), and Turkey (*Meleagris gallopavo*) were obviously detrimentally affected, while the effects of these same clearcutting operations on less conspicuous wildlife, such as songbirds, often went unnoticed. It is quite probable that the Red-cockaded woodpecker (*Dendrocopos borealis*), whose habitat requirements include a mature pine forest, was in great danger of becoming extinct at that time.

On the other hand, those species of birds that thrive in early stages of plant succession should have become very numerous in the years immediately following the clearcutting. This early state of secondary plant succession was extended for a much longer period than would have occurred naturally because of periodic burning of the range by cattlemen and others. It is well known that populations of Bobwhite quail (*Colinus virginianus*) reached high levels and were sustained for several years on these cutover lands in the South. These areas became very popular to quail hunters. Liberal hunting seasons and bag limits were the rule throughout the Southern states. As an example, on December 25, 1925, I participated in a quail hunt, along with two other hunters, on cutover land in southwest Louisiana. During this day's hunt we found 31 coveys of quail and harvested 45 birds, legally.

These high populations of quail declined significantly after forest landowners began a policy of total fire protection during the Thirties and plant succession advanced from herbaceous annuals and perennials to a brush stage. These drastic fluctuations of quail populations were very obvious to most quail hunters but little note was taken of changes in the populations of songbirds sharing similar niches.

In due time, the secondary succession of vegetation advanced to the tree stage with each sere providing favorable habitat for a somewhat different community of wildlife. Because of the interest of hunters, the rise and fall of game populations usually received much attention, but songbird populations fluctuated virtually unheeded.

As game species became scarce, hunters usually demanded that something be done by the

^{1/} Paper presented at The Symposium on Management of Forest and Range Habitats for Nongame Birds, Tucson, Arizona, May 6-9, 1975.

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state wildlife departments. Consequently, much research has been done on the life histories, habitat requirements, and management techniques of the various game animals. As a result, many industrial forest landowners, when subjected to demands by hunters were able to develop commendable game management programs on their lands.

Songbirds, in general, have not received a comparable amount of attention and research, mainly because of limited concern of the general public. Therefore little is known, outside of academia, about the techniques of songbird habitat management. Consequently, very few companies within the forest industry have any policy primarily aimed at songbird management.

There are a few notable exceptions. A number of large forest landowners in the South have adopted a specific policy having to do with red-cockaded woodpecker and bald eagle (*Haliaeetus leucocephalus*) management. Generally, these policies were adopted only after the companies were made aware of the adverse effects of their forestry practices on these species.

We who are interested in songbird management on industrial forest lands must accept several basic facts:

First, practically all industrial forest lands are managed by companies for the express purpose of producing forest products for monetary gain.

Second, good public relations are highly desirable to these companies.

Third, favorable songbird management policies should not be expected unless the company has a monetary inducement of profit or desires to improve public relations. Rarely are the policies of these companies instigated by philanthropical motives.

Fourth, there is a dearth of information on the techniques of songbird habitat management.

Therefore, it is my belief that we should not expect songbird management policies to be adopted by companies within the forest industry until we can provide them with:

1. Proper motivation, such as good public relations.
2. Reasonable, concise, songbird management techniques that can be adapted to current forestry practices.

I sincerely believe that when these two criteria have been met, most forest landowners will respond favorably.

The Current Status of State Nongame Bird Programs¹

Jack R. Grieb^{2/} and Walter D. Graul^{3/}

Abstract.--Thirty states presently have nongame programs dealing in part with birds, but only 17 have a program that includes at least one full-time nongame employee. Most states are restricted by shortages of money and manpower. As they try to alleviate these problems, they are proceeding with active nongame bird programs which include the following: (1) seeking legislation needed for management, (2) passing specific regulations, (3) conducting literature surveys, (4) documenting distributions and monitoring population levels, (5) enhancement and protection of habitat, (6) direct management activities, (7) programs to enhance the nonconsumptive use of nongame birds, and (8) public education programs.

INTRODUCTION

Historically, wildlife agencies were primarily concerned with the management of harvestable wildlife populations. The environmental movement that gained its major impetus about 10 years ago, however, is now being translated into widespread public activism. Increasing numbers of people are now demanding that a wider spectrum of wildlife be included in management programs. Although this public attention was initially focused on threatened or endangered species, it is now encompassing all nongame resources. The states are responding to these public demands with the establishment of specific nongame programs. The increased state nongame responsibilities are necessary, since within the United States the common law of the land states that "wildlife is the property of the people, the sovereignty of which they have vested with the states to be conserved and managed for the benefit of all people" (Arnett 1972a).

Before going into the details of the state nongame bird programs, "nongame" must be defined

since among the states many definitions are used. In the present paper "nongame" refers to those species or subspecies that are not hunted, harvested, or intentionally removed from the populations by humans, except for special scientific purposes or to prevent certain types of damage. Definitions of nongame in at least 14 states conform to this concept (Sandfort 1973).

RESULTS AND DISCUSSION

In February, 1975, Colorado mailed a survey form to the agency responsible for wildlife management in each of the 50 states. Of the 48 states that responded, 30 indicated that they have nongame programs dealing in part with birds, but only 17 have programs that include at least one full-time nongame employee. Interestingly, 15 states indicated that they hope to establish a nongame program within the next two years.

When comparing the state nongame programs, the following two problems are common to all: (1) how to most efficiently utilize small staffs relative to the large number of species needing attention and (2) how to obtain sufficient funds for nongame programs. Colorado's experience illustrates these two problems. Our nongame program was expanded in 1972 with the employment of a full-time nongame biologist. Since then, a nongame mammal specialist and a nongame bird specialist have been added. The 1974-75 budget for these personnel totals \$76,000.

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Our personnel problem has been partially relieved by the establishment of a Citizen's Nongame Advisory Council. The Council consists of college professors, representatives of environmental groups, and concerned citizens. The group meets once a month to provide both public input and scientific expertise into our program.

Non-Divisional help is also utilized in the collection of data. For instance, volunteers help in organized censuses on several species each year. Additionally, our efforts are coordinated with local universities in the collection of field data and literature reviews.

Even with the above help, a logical management priority system was needed to guide us in determining those species or subspecies requiring immediate attention, since our nongame bird program has the responsibility for 318 species. Our priority system is based on biological, aesthetic, legal, and moral grounds.

On the biological side, several papers in this symposium have illustrated the high degree of diversity found in some ecosystems. Although more data are needed for verification, such diversity presumably lends stability to ecosystems (MacArthur 1955; McNaughton and Wolf 1973; Odum 1971; Woodwell and Smith 1969). Additionally, some species play key roles in maintaining communities, although we are not always aware of these roles (Wagner 1974). In terms of management, this means that populations of the more common species of birds need to be maintained. As a population approaches extinction the biological justifications for maintaining it lessen since the damage is already done.

The aesthetic, legal, and moral grounds can be considered together. Aesthetically, a growing segment of the public is demanding that we maintain species and subspecies for the enjoyment of future generations. Such maintenance now is required by law in most states. Morally, many people are pointing out that all living things have a right to exist on this earth. This is not to deny that extinction is a natural process, but rather it is a realization that man has greatly accelerated this process in many cases. Thus, it is apparent that those avian species and subspecies that are endangered or likely to become so in the near future must be maintained.

How does all of this mesh into a management priority system? With limited funds, most states have chosen to place the management of threatened and endangered species as top priority because of public interest. In Colorado, we have followed the same trend, but we are also concerned with the following: (1) any avian population that is declining in Colorado and (2) any species or subspecies with a de-

clining population trend nationally, regardless of its Colorado population status. In conjunction with this priority system, the management potential of a given species or subspecies is also considered. As additional funds become available our program will be expanded to include other species.

This brings us back to the funding problem. The Wildlife Management Institute is conducting a detailed study on nongame funding, but the results are not available yet. Some of the basic funding mechanisms along with their implicit philosophies, therefore, will be considered here. The amount of money being spent annually by the states on nongame programs ranges from zero to nearly one million dollars (California). Our survey indicated that 23 states fund their nongame programs at least in part with the traditional revenues obtained from hunters and fishermen. In fact, some people feel that because sportsmen have been licensed to take wildlife, they should subsidize the nonconsumptive public by paying the entire bill for maintaining all wildlife (Arnett 1972b).

Such an attitude on the part of nonsportsmen perhaps is not unexpected, but a look at hunter attitudes is especially interesting. In Colorado, we interviewed 561 resident deer and elk hunters during the 1974 season. Ninety-two percent felt that endangered species should be managed and 80% felt that nongame in general should be managed. Eighty percent thought that nongame programs should be funded at least in part with money obtained from hunting license fees. Although this survey only involved a small percentage of sportsmen, it preliminarily indicates that sportsmen are strong supporters of nongame programs and they are willing to share in the cost of maintaining such programs.

Some states base their nongame funding on the philosophy that maintaining nongame is the responsibility of the general public since they generally benefit from nongame programs. It is further argued that hunters and fishermen already pay their fair share since habitat developed for game also supports many forms of nongame (Arnett 1972b).

The Colorado nongame program is based on the preceding view with the bulk of the financial support coming from legislative general fund appropriation, a practice shared with eight other states. We do, however, rely on game cash funds indirectly for providing administrative services, office space, and field personnel (Wildlife Conservation Officers). In addition, Pittman-Robertson funds support a Peregrine Falcon (Falco peregrinus anatum) recovery project.

General fund appropriations, however, are somewhat unstable because of the economic and political variables. Some states, consequently, have sought other, more stable funds. Ohio initiated a Wildlife Conservation Stamp Program in 1972 with the stamp selling for five dollars. Through 1974, 2,206 stamps were sold for \$11,030.00. Colorado began a similar project in 1974 and in the first year over 800 stamps were sold, netting about \$2,500. It is apparent that a voluntary stamp program will never generate large sums of money, i.e. how many hunting and fishing licenses would be sold if they were not required? Nonetheless, these programs should be continued, since they have made many people aware of state nongame programs and they allow concerned individuals to contribute funds for projects which benefit all citizens.

In 1972 California enacted an Environmental Protection and Research Act which provided money for environmental programs through the sale of personalized license plates. Part of this money has gone towards the management of threatened and endangered species (Arnett 1972b). Washington also initiated a personalized license plate program with all of the profits going into their nongame program.

Oregon is experimenting with a system aimed at the nonconsumptive public. On their Sauvie Island Wildlife Area a small use fee is charged for those who do not possess a hunting or fishing license (Shay 1975). The special fee has not generated much money, but it may have potential if applied on a large scale.

Because of the overall funding problem, most states are searching for additional funding mechanisms. One of the most popular proposals is some type of special tax. This has definite possibilities, as illustrated in Minnesota where a two cent per pack tax on cigarettes goes into a natural resource fund (Hertz 1971). Massachusetts has a bill before their present legislature that would authorize a 3% tax on bird seed. If it passes it is estimated that the tax could generate about \$300,000 annually for their proposed nongame program.

Additionally, Congress enacted The Endangered Species Act in 1973 which is intended to provide federal funds to the states on a cost-sharing basis. Although many states stand ready to use such funds, Congress has not appropriated money for use by the states (Williamson 1974). The states, consequently, are urging Congress to take action so that the intent of the 1973 legislation can be carried out.

Despite the preceding problems, the states are proceeding with active nongame bird programs. One of the first steps taken has been the enacting of legislation to enable them to properly manage nongame, especially threatened or endangered species. A survey conducted by Richard Denney, of our Division, in 1973 showed that 25 states had laws to protect endangered species and 11 others were considering such legislation.

Once states have obtained the basic legislation necessary to manage nongame species, they have been able to initiate specific regulations to benefit nongame birds. For instance, in Colorado the Wildlife Commission has the authority to restrict hunting in any area of the state if Whooping Cranes (Grus americana) are present.

Another Colorado example involves the White Pelican (Pelecanus erythrorhynchos). We have a nesting population that utilizes an island on one reservoir in northeastern Colorado. This species apparently will not tolerate much human activity near its nesting areas (Sloan 1973), so a regulation was passed that prohibits boats from approaching closer than one-quarter mile of our nesting island during the breeding season.

Some state regulations are directed at scientists. As populations reach critically low levels, collecting is usually prohibited and these prohibitions seem to be on the increase. For example, Richard Todd, of the Arizona Game and Fish Department, recommended that 12 species of birds be added to the list of Arizona birds for which a scientific collecting permit will not be issued (Todd 1970).

It appears that additional regulations to protect nongame birds will be necessary in the future. This is especially applicable for species or subspecies with low population levels since these seem to be the focal points of much public interest. For instance, in Colorado the spring population of the Greater Prairie Chicken (Tympanuchus cupido pinnatus) is now estimated to be about 600, restricted primarily to one county. Formerly, this species nested over a 15-county area in Colorado. The past two springs many people visited the booming grounds and this is causing problems. The well-meaning visitors disrupt the courtship activities and, more importantly, they sometimes trespass on private property, thereby creating landowner hostilities.

The latter problem is not unique to Colorado, and other agencies have taken steps to correct such situations. In Nebraska, observation blinds are provided near some Sharp-tailed Grouse (Pedioecetes phasianellus)

booming grounds on federal land, thereby reducing the likelihood of people trespassing on private land (James Webb, pers. comm.). Similarly, the Arizona Sonora Desert Museum, in Tucson, provides blinds for night photography while people are restricted from other areas. Thus, the combined actions of restricting people from certain areas while providing alternative observational areas may have widespread application in the future.

State nongame bird programs, however, include more than just legislative and regulatory activities. Most states devote considerable time and effort in documenting distributions and in monitoring population levels. This field work is necessarily accompanied by extensive literature reviews.

Two of the most comprehensive survey programs are being conducted by California and Arizona. California has organized a statewide shorebird survey, utilizing many volunteers (Jurek 1974), and the study has included an excellent literature review (Gerstenberg and Jurek 1972). Arizona has conducted a literature review of 261 birds in conjunction with their field work. They have compiled considerable distributional and density data on birds with the emphasis being on riparian habitats (Todd 1969, 1970).

States also are involved with programs to enhance or protect nongame bird habitat. A good example of habitat enhancement involves the Colorado nesting population of White Pelicans. Unfortunately, the sandy nesting island was severely eroded over a period of several years. In 1974, the island was repaired and another island was constructed on a nearby reservoir in hopes pelicans would utilize it for nesting in the future.

Hawaii initiated one of the first nongame bird habitat protection programs with the establishment of seabird sanctuaries. Other states have similar programs and Colorado has a general land use law (HB 1041) that requires county commissioners to consider wildlife before issuing permits for development. The Colorado Division of Wildlife has the responsibility of providing the wildlife data and nongame birds are included with special attention being given to threatened and endangered populations. With this law we have been successful in protecting some crucial nongame bird areas and it is hoped that even more success will be realized in the future.

One final management project will be used to illustrate the scope of state programs designed to aid nongame birds. Our Division is cooperating with Cornell University and several other agencies in conducting a

Peregrine Falcon (Falco peregrinus anatum) breeding project. The project involves breeding the birds in captivity near Fort Collins, Colorado, and releasing the offspring in several states. This is considered a nongame program because of the endangered status of this species although raptors, in general, are considered sport game (falconry) in Colorado.

In some cases the nongame interests of state wildlife agencies conflict with other interests within the organization. The conflict between maintaining the Colorado nesting colony of White Pelicans and boating interests has already been mentioned. Similarly, the Greater Sandhill Crane (Grus canadensis tabida) nests in northwestern Colorado, and these birds frequently rest and feed in the upper end of Steamboat Lake during the summer. This lake is the site of a State Park which accommodates many boaters, so buoys are used to prevent boats from disturbing the cranes.

When these conflicts of interest do occur solutions are not always easy, since it is presently difficult to relate the value of a nongame population to an established recreational activity. States, consequently, are in need of data which reflect the monetary and recreational values of nongame. These values are admittedly hard to determine, but there is a preliminary indication they may be higher than previously suspected. For instance, the feeding of wild birds may represent a fifty million dollar annual industry in the United States (DeGraaf and Thomas 1974).

All of the preceding discussion relates to programs that are designed to directly benefit the nongame resource. State nongame programs, however, also include activities designed to benefit the public. For instance, Arizona is preparing a recreational guide to the nongame birds and mammals. Washington has plans to hire an urban wildlife biologist and 12 states have programs to encourage the preservation and development of wildlife habitat in urban areas to meet the nonconsumptive needs of people. One problem in this area is that states are not fully aware of nonconsumptive demands of the public. At least 13 states, therefore, are in the process of surveying public attitudes towards nongame programs.

It is logical that state wildlife agencies should share the responsibility of educating the public regarding nongame since these agencies include scientists with particular expertise in this area. Not surprisingly, therefore, 20 states indicated in our survey that they were involved in public education programs. In Colorado, we have produced a film dealing with threatened and endangered species that is available to the public. The biggest

need, however, is to enlighten the public on the biological reasons for maintaining nongame.

In closing we would like to relate what has been said thus far to what can be expected in the future. The nongame public education activities being conducted presently by the states and other agencies should result in even more public support for the expansion of nongame bird programs. As this expansion occurs, the states will need to maintain flexible positions so that every opportunity can be exploited to provide realistic, aggressive nongame bird management programs.

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The Bureau of Land Management Wildlife Habitat Management Program, with Special Emphasis on Nongame Bird Habitats¹

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Abstract.--The Bureau of Land Management (BLM) administers wildlife habitat on 451 million acres of national resource lands (NRL). The economic value of the "harvested" wildlife resource on these lands was estimated as \$350.7 million in 1973, but could be as much as \$4.6 billion by the year 2000. However, wildlife habitats on the NRL are producing far below potential. The BLM intends (a) to provide stabilization of unsatisfactory or declining habitats and (b) to protect, enhance, and intensify management on all NRL. New mandates through which this may be possible are discussed. Examples of nongame bird habitat projects, such as the Snake River Birds of Prey Natural Area, the Blanca Wildlife Habitat Area, and the San Simon Cienega Wildlife Habitat Area, illustrate the habitat management capabilities of the Bureau. Greater opportunities for positive wildlife habitat management programs on the NRL are developing from the BLM planning system.

WILDLIFE HABITAT ON THE NATIONAL RESOURCE LANDS

The Bureau of Land Management (BLM) is charged with protecting, maintaining, and enhancing aquatic and terrestrial wildlife habitat on some 451 million acres collectively called the national resource lands (NRL). By acreage the BLM has the largest land management responsibility in the Nation.

This paper deals primarily with the ten contiguous Western States in which the BLM has significant land holdings (Table 1). Virtually

all of the 174 million acres of NRL in these States support wildlife with varying potentials for habitat protection, maintenance, and enhancement. Included are over 112 million acres of big game habitat, 129 million acres of small game habitat, and 600 thousand acres of waterfowl nesting and wintering grounds (Table 2). The NRL in the ten contiguous Western States also include over 243,000 acres of lakes, 331,000 acres of reservoirs, and 18,274 miles of streams (Table 3).

^{1/} Paper presented at The Symposium on Management of Forest and Range Habitats for Nongame Birds, Tucson, Arizona, May 6-9, 1975.

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The numbers of antelope, bighorn sheep, deer, and elk that use these habitats at some time during the year are listed in Table 4. But these lands also double as nongame habitat--in most cases as nongame bird habitat, the subject of this symposium.

Table 1.--Acreages in the ten Western States with the largest BLM land holdings (excluding Alaska)*.

State	Total Acres	BLM Administered	% BLM
Arizona	72,901,760	12,586,604	17.3
California	101,563,520	15,584,859	15.3
Colorado	66,718,080	8,331,857	12.5
Idaho	53,476,480	12,020,278	22.5
Montana	94,168,320	8,141,434	8.7
Nevada	70,745,600	48,417,627	68.4
New Mexico	77,866,240	12,948,416	16.6
Oregon	62,067,840	15,732,001	25.4
Utah	54,346,240	22,641,424	41.7
Wyoming	62,664,960	17,543,148	28.0
Total	716,519,040	173,947,648	24.3

*Data from Bureau of Land Management (1974a).

Table 2.--Estimated acres of important game and waterfowl habitat on the NRL, 1974*.

State	Big Game	Small Game	Waterfowl
Arizona	7,898,000	11,442,000	2,500
California	5,187,000	10,442,000	1,314
Colorado	8,000,000	6,653,000	25,000
Idaho	9,333,600	11,440,600	140,600
Montana	7,000,000	5,077,000	162,500
Nevada	21,618,000	23,270,000	38,500
New Mexico	9,819,000	15,240,000	18,000
Oregon	10,770,000	12,579,000	83,800
Utah	17,575,000	18,926,000	37,000
Wyoming	15,013,000	14,021,000	90,000
Total	112,213,600	129,182,600	599,214

*Data from Bureau of Land Management (In Prep.).

Table 3.--Estimated miles or acres of existing fishing streams, lakes, and reservoirs on the NRL, 1974*.

State	Acres of Lakes	Acres of Reservoirs	Miles of Stream
Arizona	1,616	26,975	378
California	56,137	22,428	520
Colorado	8,199	13,822	1,498
Idaho	134,598	92,134	3,275
Montana	578	44,189	688
Nevada	23,976	18,305	1,066
New Mexico	630	298	42
Oregon	5,719	81,209	7,226
Utah	683	15,121	2,046
Wyoming	<u>11,145</u>	<u>16,303</u>	<u>1,535</u>
Total	243,281	330,784	18,274

*Data from Bureau of Land Management (In Prep.)

Table 4.--Estimated numbers of selected big game animals using NRL, excluding Alaska, 1974*.

State	Antelope	Bighorn Sheep	Deer	Elk
Arizona	230	3,340	32,850	50
California	34,914	1,253	215,800	550
Colorado	8,411	509	235,716	45,666
Idaho	9,600	375	68,150	6,050
Montana	23,926	411	110,100	3,584
Nevada	3,508	3,350	184,100	500
New Mexico	6,275	44	37,560	1,014
Oregon**	9,205	265	274,530	9,525
Utah	2,950	250	164,000	1,100
Wyoming	<u>91,650</u>	<u>885</u>	<u>135,150</u>	<u>27,380</u>
Total	190,669	10,682	1,457,956	95,419

*Data from Bureau of Land Management (In Prep.)

**Includes Washington.

The economic value of the "harvested" wildlife resource on the NRL in 1973 has been estimated at \$350.7 million:

<u>Commodity</u>	<u>Value</u> <u>(Millions)</u>
5,806,000 Hunter Days @ \$10.52 ea.	\$ 61.1
Meat Value of Game -- 30.3 Million lb. @ \$1.00/lb.	30.3
6,593,000 Fisherman Days @ \$6.30 ea.	41.5
Meat Value of Sport Fish -- 9.9 Million lb. @ \$1.00/lb. (Assuming Average Daily Catch of 1.5 lb.)	9.9
Non-consumptive Use -- 28,233,000 Camping, Picnicking, and Sight- seeing Use Days @ \$3.84/day (See Text)	108.4
Meat Value of Commercial Fish @ \$1.00/lb.	<u>99.5</u>
Total	\$ 350.7

This represents a 135 to 1 return on the Bureau's \$2.6 million wildlife expenditure during FY 1973. Furthermore, due to inflation, this is a conservative estimate because it is derived from 1973 NRL recreation visitor-day and game harvest statistics (Bureau of Land Management 1974a) and 1970 figures for hunter and fisherman day values (Fish and Wildlife Service 1972).

The value of non-consumptive use is based on the assumption that most camping, picnicking, and sightseeing on the NRL is (a) directly related to wildlife appreciation, or else (b) the quality of such outdoor experiences are significantly enhanced by the presence of wildlife. The value of \$3.84 placed on a day of non-consumptive use is based on the percentage (52.1%) of the 1970 average hunter and freshwater fisherman day value (\$7.38) spent on food, lodging, transportation, and auxiliary equipment (Fish and Wildlife Service 1972). This excludes hunting equipment, guides, dogs, licenses, and privilege fees that a non-consumptive user of wildlife on the NRL would not need to purchase.

Public use and recreation on the NRL is expected to increase by about 10 percent per year over 1973's 45 million recreational visitor days. If quality wildlife-related recreational experiences can be supplied to recreationists through the year 2000, the annual value of the

NRL's wildlife resource will increase thirteen-fold--to \$4.6 billion.

To many, putting a price on a deer's head or on a complete wildlife resource probably cheapens it. The alert citizen "values wildlife more as a matter of principle than as a commodity" (Advisory Committee on Nongame Wildlife Policy 1974). But economics is a fact of life. Not until one begins speaking in terms of millions annually is the value of wildlife and wildlife habitat actually comprehended by the controllers of resource management dollars.

THE BLM WILDLIFE PROGRAM

Modes of Operation

Today, accomplishments for wildlife on the NRL are joint efforts involving the BLM, State game and fish agencies, and the other Federal agencies. Responsibilities have been formalized with all Western States by Memoranda of Understanding. The BLM is primarily responsible for the habitat, and the State agencies are responsible for fish and wildlife populations.

In order to accomplish significant objectives for wildlife, the BLM's Wildlife Habitat Program is operated within the Bureau's planning system. This system provides an objective and standardized process for making land-use decisions in advance of on-the-ground actions.

With guidance from the planning system, Activity Plans are developed. In the case of wildlife habitat, terrestrial and aquatic Habitat Management Plans (HMP's) are written to provide a firm basis for on-the-ground enhancement. This might involve fencing riparian habitat or an upland meadow to exclude livestock. HMP's are also developed to specify management goals, methods, and objectives for the many BLM Wildlife Habitat Areas, such as the Blanca in Colorado or the San Simon Cienega in Arizona and New Mexico (see below).

The BLM Wildlife Program also provides input into the Activity Plans, environmental analysis records, and impact statements of other BLM programs, such as Range, Watershed, Recreation, Minerals Management, and Lands and Realty. This significant investment of time and manpower has produced many benefits for wildlife. The following are a few examples involving nongame birds. In New Mexico a proposed lease involving millions of dollars worth of strippable coal was denied because of the presence of nesting prairie falcons. On the west coast, habitat for spotted owls is being inventoried for possible exclusion from timber harvesting. In Alaska, at the insistence of the BLM, the Federal Aviation Administration

has placed restrictions on the use of an airport near a peregrine falcon eyrie. In Idaho, a moratorium has been placed on the process of Desert Land Entry within five miles of the Snake River Birds of Prey Natural Area. Throughout the West, the BLM is placing stipulations on powerline rights-of-way approvals to prevent electrocution of eagles and other large perching birds. The broadening of the Bureau's Wildlife Staff to include additional nongame expertise indicates that even greater opportunities for similar promotion of wildlife habitat protection on the NRL will exist in the future.

Goals

Long-range objectives of the BLM Wildlife Program include the following:

- (a) To provide stabilization for unsatisfactory or declining habitats;
- (b) To enhance and intensively manage wildlife habitats, especially those of threatened or endangered species;
- (c) To increase wildlife input into other resource programs so that wildlife values are considered and provided for in program development and implementation; and
- (d) To sustain an overall wildlife habitat management program on all NRL that is responsive both to wildlife needs and public demands, including a progressive balancing of the Bureau's Wildlife Program as it relates to game versus nongame species.

Meeting both wildlife needs and public demands taxes the land manager's skills. The great challenge is twofold: (a) to manage renewable resources in a manner that ensures balanced use of the land to meet the Nation's food, fiber, and recreational needs of future generations, while (b) managing the extraction of non-renewable resources in a manner that ensures the least harmful impact on the quality of the environment. The well-being of the NRL's wildlife, a renewable resource, depends on how well that challenge is met--in short, how adequately the BLM Wildlife Program is funded; how widely older legislation is interpreted; how efficiently and effectively recent Acts and Executive orders are implemented; and how soon the Organic Act is passed.

New Mandates--An Opportunity to Achieve Program Balance

Program balance--be it within the Wildlife Program or between the various BLM Divisions--

is a key philosophy within the Bureau as emphasized by Director Berklund. He spoke of "Striking a Balance for Land Management" in Pittsburgh recently, noting that the BLM has had a history of management without sufficient manpower and funds. However, we are optimistic about the possibilities for improved habitat management in light of new and pending legislation, and new responsibilities given to the BLM by the Secretary of the Interior. Three mandates are of particular importance and timeliness today.

First, the cause of nongame wildlife has been bolstered in recent years through growing public concern for endangered species, culminating in the passage of the Endangered Species Act of 1973 (P.L. 93-205). Of the 48 endangered fish, reptiles, birds, and mammals that occur in the 11 Western States and Alaska (Fish and Wildlife Service 1974), 29 are found or are suspected of occurring on the NRL. In addition, the Smithsonian Institution (1975) has suggested that over 1,000 species of plants be listed as threatened or endangered in the 10 contiguous Western States where the BLM has large holdings. When plants and threatened animals are finally listed, habitats of several hundred such species--from butterflies to cactuses--will require long-term monitoring, enhancement, and general management by the BLM.

The BLM has just completed an analysis of Bureau operating procedures and on-the-ground actions that might present conflicts with the intent of the Act. One spinoff from this analysis was the identification of several non-threatened species that require strong consideration before land-use actions are taken by the BLM. These species include the desert tortoise, ferruginous hawk, spotted owl, prairie falcon, bighorn sheep, Mohave ground squirrel, Tule elk, and others. The Bureau intends to do its part in managing habitat to keep these and other nongame species from declining in numbers so that listing as threatened or endangered becomes the only avenue for their protection.

As for currently endangered species, the BLM has outlined three important steps to be taken to develop an effective Bureau program:

- (a) alignment with the nationwide coordination efforts of the FWS;
- (b) maintenance of a supportive role (technologically, financially, and with manpower) in State endangered species programs in cooperation with the States, and
- (c) development of an active, positive Bureau program both to implement Recovery Plans and to make listings of other species unnecessary.

The second new mandate for the BLM Wildlife Habitat Management Program is the Sikes Act (P.L. 93-452). This Act gives the Bureau responsibility to develop and implement (in cooperation with the States) conservation and rehabilitation programs for wildlife on those lands administered by the BLM. In this context, the Sikes Act extension for wildlife has been called a "BLM Organic Act for Wildlife." The existing BLM and State planning systems will expedite on-the-ground implementation of the Sikes Act through Habitat Management Plans based on multiple-use recommendations and decisions developed by the planning system.

Proposed guidelines for implementation have been reviewed and commented upon by BLM State and Washington Office staffs and are presently being revised. These guidelines address such matters as (a) tie-in of conservation and rehabilitation programs with the existing State and BLM planning and program management systems, especially with the BLM's Wildlife Habitat Management Plans; (b) cooperative agreements and supplements to existing Memoranda of Understanding between the BLM and each State Game and Fish agency in the Western States; and (c) coordination with other BLM programs, the FWS, and the USFS.

A third new responsibility was given to the BLM in February of this year: administration of the Kofa, Charles Sheldon, and Charles M. Russell National Wildlife Ranges. This action has caused some concern among conservation groups. Some see it as a threat to our national wilderness system. Others, remembering the BLM's past identification with the single purpose Grazing Service, have charged that the action was a "sell out" to livestock and mining interests. However, both the Secretary of the Interior and BLM Director Berklund have assured the public that these ranges will be managed for the primary benefit of wildlife as defined in the initiating Executive orders. This has good implications for both game and nongame wildlife on the areas. All other resource uses will be subordinate to and will not conflict with wildlife. Furthermore, wilderness areas will be managed under the principles of the Wilderness Act. The BLM, with its broad and growing spectrum of resource management expertise, can and will manage these wildlife habitats effectively.

THE BLM'S MAJOR ACCOMPLISHMENTS FOR NONGAME BIRDS

Expenditures for Nongame Species

During FY 1974, the BLM spent just under \$200,000 (out of a total wildlife budget of \$3.4 million) on nongame wildlife habitat

(Bureau of Land Management 1974b). This included habitat inventory, basic research, planning, and on-the-ground management. About \$50,000 of this was spent directly for nongame bird habitat study and preservation. This proportion is certainly greater in FY 1975 because of increased funding of research in the BLM's Snake River Birds of Prey Natural Area in Idaho, one of the Bureau's more successful wildlife programs (see below). Though the percentage for all nongame wildlife is still small by comparison to expenditures for game species, a steady balancing is a major goal as indeed it must be in response to public demands for both consumptive and non-consumptive wildlife use.

The Snake River Birds of Prey Natural Area

This 26,255-acre (41-square-mile) sanctuary (Fig. 1) was withdrawn in 1971 from all forms of appropriation under the public laws, including the General Mining Law (30 U.S.C. Ch. 2) and the Desert Land Entry Act (43 U.S.C. 321-323) as amended. This land action on behalf of wildlife by then Secretary of the Interior Rogers C. B. Morton has but one exception: leasing under the mineral leasing laws.

Golden eagles and prairie falcons are the key species inhabiting the Natural Area, though the canyon contains one of the densest



Fig. 1 Snake River birds of prey natural area.

populations and finest arrays of breeding raptors in North America--and perhaps the world. The following number of breeding pairs--about five pairs per square mile--were found on the area in 1973:

Species	Breeding Pairs
Golden Eagle	14
Prairie Falcon	112
Red-tailed Hawk	27
Marsh Hawk	6
Kestrel (Sparrow Hawk)	17
Ferruginous Hawk	5
Great Horned Owl	9
Barn Owl	19 (Est.)
Screech Owl	2
Burrowing Owl	2
Total	213

The BLM is confident that studies of these birds now in progress will allow better land management to benefit endangered as well as abundant raptors in similar habitats throughout the world.

The raptor management problems that these studies address have developed because of two major gaps in our knowledge of predatory birds: (a) most raptor research has been seasonal and short-term; and (b) studies of population dynamics and food habits of raptors usually have not been conducted simultaneously with quantitative studies of prey population levels and other ecological considerations. A multifaceted, penetrating research effort must be made if quantitative data concerning population dynamics, ecological impact, management, and conservation are to be synthesized.

During a five-year period, BLM Wildlife Biologists, and contracted private consultants and university personnel, will conduct at least seven closely coordinated studies.

Titles and principal investigators (P.I.) are listed below:

- I. Population Dynamics, Reproductive Biology, and Food Habits of Raptors. BLM Wildlife Biologists; P.I. Michael N. Kochert.
- II. Estimation of Raptor Tolerance to Human Disturbance. To Be Initiated FY 1976.
- III. Activity, Hunting Patterns, Territoriality, and Social Interactions of Birds of Prey. Western Illinois Univ.; P.I. Dr. Thomas C. Dunstan.
- IVA. Density and Species Composition of Small Mammals, Birds, and Reptiles. Utah State Univ.; P.I. Dr. John Neuhold and Dr. Michael L. Wolfe.

- IVB. Dynamics of Predation Upon a Raptor Prey Base. Idaho Coop. Wildlife Research Unit, Univ. of Idaho; P.I. Dr. Maurice G. Hornocker.
- V. Population Ecology of the Townsend Ground Squirrel. Univ. of Idaho; P.I. Dr. Donald R. Johnson.
- VI. Inventory and Analysis of Critical Peregrine Falcon Habitat in Regard to Possible Reintroduction in Idaho. Morland W. Nelson, Private Consultant.
- VII. Raptor Nesting and Feeding Behavior. Univ. of Idaho; P.I. Dr. Steven R. Peterson.

In addition, the Bureau will (a) determine archaeological values within the perimeter of the Natural Area, (b) survey and establish boundary monuments on the 85-mile border, and (c) maintain and/or enhance the Natural Area for the benefit of all wildlife species and for the enjoyment of the American public. When all studies are underway, annual expenditures, including "in-house" commitments and contract studies, will exceed \$200,000 per year.

The San Simon Cienega Wildlife Habitat Area

This 27,721-acre (43.3-square-mile) area along the Arizona-New Mexico border between Tucson and Las Cruces (Fig. 2) is one of the

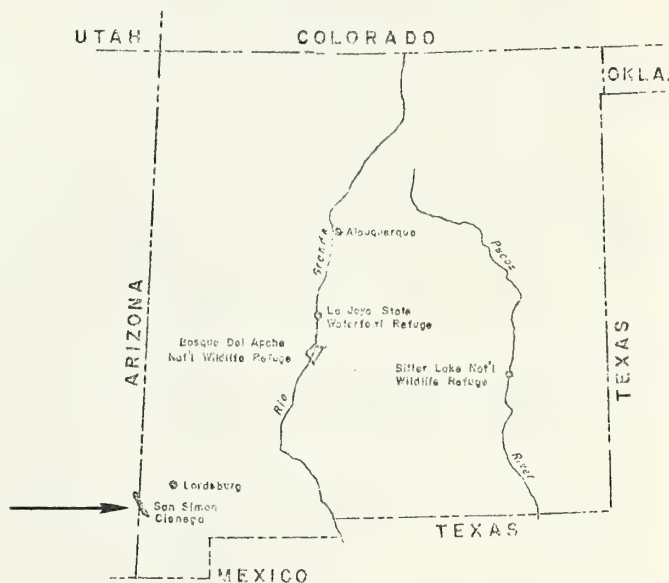


Fig. 2 San Simon Cienega, on the Arizona-New Mexico state line.

few remaining areas in the United States capable of supporting the Mexican duck. Continued loss of waterfowl habitat due to drainage of marshes, channelization of the Rio Grande, and other agricultural practices has resulted in the Mexican duck's present status as an endangered species. Of particular importance was the cessation of flow in San Simon Creek in 1952, a probable result of three years of pumping of subsurface water for irrigation.

About 200 acres of this area--a series of key ponds and associated marshes--has been withdrawn for protection of Mexican duck habitat. Management efforts include well and pipeline developments; pond remodeling; small dam construction; cover and food seedings; and fencing to exclude livestock grazing. Mexican duck production at San Simon Cienega increased from zero in 1967 to about 20 in 1969 following release of 75 birds as initial brood stock. Production has since declined steadily in the absence of additional transplants. Thus the project is currently entering a maintenance and evaluation phase before further development is undertaken.

Wildlife habitat on the San Simon Cienega has also been improved for other nongame birds. The chance of seeing such peripheral species as the masked duck or the zone-tailed hawk has made the area nationally significant for bird-watching. Several universities use the Cienega for field trips as well as a study area.

Nongame Aspects of the BLM's Wildlife Public Awareness Program

The BLM's thrust in this area has centered on four approaches: (a) individual participa-

tion in conferences, meetings, community gatherings, etc.; (b) publication of a series of technical notes on endangered or potentially threatened species; (c) publication of information brochures and Habitat Management Plans concerning specific projects; and (d) publication of field checklists of amphibians, reptiles, birds, and mammals in as many BLM Districts as possible. Progress is being made with all approaches.

The technical note series has been particularly successful with between 1,500 and 2,500 copies of each report now in circulation in the United States and abroad. The reports are literature reviews, including considerations of the management aspects of each species, followed by lists of knowledgeable scientists, concerned governmental agencies and citizens' groups, and pertinent literature. You are invited to order these reports from our Denver Service Center. Nine of the thirteen reports now available deal with nongame birds--all raptors (Table 5).

INFORMATION NEEDS OF THE BLM WILDLIFE HABITAT MANAGEMENT PROGRAM

Most types of information needed by the BLM Division of Wildlife have one major characteristic in common: they must be applicable to resource management and the accompanying decisionmaking process. For example, knowledge of both the beneficial and adverse effects of pinyon-juniper chaining, mesquite spraying, sagebrush control, seeding with mixtures as opposed to only crested wheatgrass, is of tremendous value to the Bureau. Too many of the basic research studies being done today simply cannot be put to work on the ground.

Table 5.--List of unique and endangered species technical notes.*

Ordering Number	Report Number and Species	Pages
T/N - 167	Report No. 1, Peregrine Falcon	35
T/N - 168	Report No. 2, Black-footed Ferret	23
T/N - 169	Report No. 3, Blunt Nose Leopard Lizard	13
T/N - 170	Report No. 4, Spotted Bat	13
T/N - 171	Report No. 5, Bald Eagle	58
T/N - 238	Report No. 6, Kit Fox	24
T/N - 239	Report No. 7, Golden Eagle	52
T/N - 240	Report No. 8, Prairie Falcon	18
T/N - 241	Report No. 9, Gyrfalcon	14
T/N - 242	Report No. 10, Spotted Owl	22
T/N - 250	Report No. 11, Burrowing Owl	25
T/N - 254	Report No. 12, Osprey	41
T/N - 255	Report No. 13, Ferruginous Hawk	23

* Reports available free of charge from Bureau of Land Management, Division of Wildlife (360), Denver Service Center, Denver Federal Center, Denver, Colorado 80225.

Some of the important nongame species-land management relationships that need to be explored by and for the BLM in the coming years include (1) the effects of harvesting old growth timber on the nesting of spotted owls; (2) the effects of livestock grazing on certain endangered species and riparian habitats; and (3) the effects of various patterns of pinyon-juniper leave areas on the nesting of raptors, particularly the nesting of one of North America's most unique hawks, the ferruginous hawk.

Two examples of studies the BLM has funded to gain information applicable to resource management are (1) the Snake River Birds of Prey Natural Area (see above), where one issue is whether or not to continue land disposal for agricultural development near an expanse of spectacular wildlife habitat and (2) the Winnett, Montana, study of the ecological effects of chemical and mechanical sagebrush control.

The Winnett study was a ten-year research effort involving the Montana Fish and Game Department, local universities, and the BLM. Emphasis was placed on sage grouse, antelope, mule deer, small mammal, and nongame bird use of treated and control plots of sagebrush. The details of the nongame bird aspects of these studies are available elsewhere in the literature (Feist 1968, Best 1970, Best 1972). Dozens of miscellaneous reports, 19 journal publications, 12 theses and dissertations, and a movie have resulted from other aspects of this study.

Another critical information need of the BLM is a system of standardized techniques for Bureauwide use to analyze the habitats of all categories of wildlife, including nongame species. These techniques must be economical in terms of manpower and funding, effective in providing sufficient data, yet flexible to allow widespread use in a variety of habitats. We envision the capability to make inter-site comparisons such as has been done in recent years in the International Biological Program, Grassland Biome Project.

Properly applied by the land manager, the concept of inter-site comparison could provide a means of rating NRL wildlife habitats as to faunal uniqueness, non-consumptive value, and recreational value in an effort to balance these considerations with economic or agricultural values in the interest of multiple-use management. Thus to aid day-to-day management of the NRL, habitat analysis techniques should produce data which can accommodate set procedures for utilizing floral-faunal relationships

in making decisions. The development of such techniques and procedures will be a major thrust of the Bureau's Denver Service Center Wildlife Staff, including two new Wildlife Management Biologists specializing in nongame species.

A more specific information need of the BLM is knowledge of endangered species habitats on the NRL. The Bureau cannot protect a peregrine falcon eyrie or a pupfish pond it knows nothing about. And all responsible Federal agencies combined could not fund complete inventories of all endangered species. We need the assistance of State agencies and the public to avoid duplication of effort and to hasten the next step--habitat management for endangered species.

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National Forest Nongame Bird Management¹

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Abstract.--Forest Service policies and decisions related to nongame bird management programs are presented. Examples of significant programs for threatened and endangered species are discussed as well as other nongame bird activities.

INTRODUCTION

I want to thank you for the opportunity to speak at this symposium. I am particularly pleased to be part of a program on nongame wildlife management, which I think is one of the major challenges facing the wildlife management profession today.

I also wish to express my appreciation to the following Forest Service people who provided assistance and information for this report: Roger S. Bumstead, David J. Dunaway, Herman L. Holbrook, Norman R. Howse, Dale A. Jones, Charles Kennedy, Leon W. Murphy, Sigurd T. Olson, Robert E. Radtke, Paul W. Shields, Donald D. Strode, and Dale L. Willis.

National Forest wildlife habitat programs in the past have sought to maximize the production of game species. The emphasis was placed on the commodity production, and even that was mostly for big game species. This was not necessarily wrong, considering the spectacular expansion of deer herds we were facing in the early 1950's. We did not foresee the new wave of public awareness for the environment, and greatly broadened concern for all wildlife that has swept the nation.

The Forest Service policy is to develop an effective balanced program for all wildlife and fish species. The exploding public interest is obvious, but research and a sound data base for management programs are lacking for many species.

The key to planning the management for all species of wildlife is to know the species habitat requirements and provide a variety of habitat components in a desirable combination that will meet the needs of as many species as possible.

The principle of "diversity" is basic in the development of management programs which consider all species as a group instead of individual species and which do not favor one species at the expense of some other.

One of the interesting social phenomena of our time is that sport hunting of wild animals has, almost overnight, become unacceptable to increasing numbers of people in our society nationwide. In 1972, more than 9 million visitor-days of use^{3/} by big game hunters and more than 4 million by those searching for small game were recorded on National Forest lands. Significantly, we estimated that nature observers and wildlife photographers chalked up nearly 18 million visitor-days on the National Forests in 1971. Obviously, more and more people come to see and photograph wildlife than to hunt it. Thus, we see an increasing value and appreciation for nongame birds.

Optimum forest wildlife populations are attained in a habitat consisting of a mosaic of forest stands in various stages of succession interspersed with openings. Most species of nongame birds are "edge" dwellers, living along the lines where two distinct types of cover merge (Jahn 1974).

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^{3/}Use expressed in visitor-days as provided in Recreation Inventory Management (RIM). For example, each hunter visitor-day represents the equivalent of one person hunting for 12 hours or 12 persons hunting for 1 hour.

FOREST SERVICE POLICIES RELATED TO NONGAME BIRDS

1. Cooperate with State Conservation Departments as well as with the Fish and Wildlife Service, Bureau of Land Management, and other Federal agencies.
2. Develop "appreciative" visitor use of wildlife through programs which encourage bird and animal watching, photography, nature walks, and general observation of all forms of wildlife and fish.
3. Recognize the importance of the 39 endangered wildlife and fish species found on or near National Forests in the Nation.
4. Manage and protect wildlife and fish habitat on National Forests in several ways: through coordination with other land development activities, through direct habitat improvement projects, and through cooperative habitat improvement programs with State Conservation Departments.

DIRECTION

The Forest Service will:

1. Determine the location and extent of development of habitats for various fish and wildlife species.
2. Favor indigenous wildlife species, both game and nongame, over exotic species and natural-habitat management procedures over artificial.
3. Establish wildlife and fish habitat as the primary use on limited areas of land or water which are key to survival for:
(1) endangered species, (2) threatened species, (3) species which depend upon National Forest lands for a major portion of their habitat, and (4) other species which depend upon limited areas of seasonal range for survival.
4. Involve all interested individuals, groups, and organizations in wildlife habitat policies and programs.
5. Act in accordance with policies, goals, and direction contained in the National Environmental Policy Act.

Our definition of wildlife is "all non-domesticated mammals, birds, reptiles, and amphibians living in a natural environment, including both game and nongame species, whether considered beneficial or otherwise."

In recent years, Forest Service programs related to nongame birds have received

considerable attention. Forest resource managers have recognized the commonly expressed desire of the people to appreciate and perpetuate nongame species. I think that we would agree that much needs to be learned about habitat management for these species before we can be fully satisfied with the information base. However, habitat management and improvement for nongame species is underway and considerable progress has been made in some areas. Some of the most significant Forest Service programs nationwide are presented.

ENDANGERED AND THREATENED NONGAME BIRDS

The 13 bird species, listed by the Department of Interior's Office of Endangered Species, found on or near National Forest System lands will receive special protection and management of their habitat. Considerable progress has already been accomplished on four of these endangered birds: the Kirtland's warbler, Red-cockaded woodpecker, California condor, and the Puerto Rican parrot. We have completed preliminary habitat inventory work on the threatened spotted owl found in California and Oregon.

In 1972, the Southern Region of the Forest Service, USDA, entered into a contract with E. Burnham Chamberlain, the Charleston Museum, to conduct a survey of rare, endangered, and unique birds of the Southern National Forests. Information was obtained on distribution and occurrence, population estimates, life history, habitat requirements, and management recommendations. Information was obtained on 23 species. The Southern Region has given particular attention to the Red-cockaded woodpecker (Dendrocopos borealis). This species, closely associated with Southern pines, since 1800 has decreased because of habitat alteration. Forest Service management is primarily concerned with providing suitable nest and roost trees and habitat to supply food needs. Cavity trees and support trees are retained as well as sufficient foraging area.

The Kirtland warbler (Dendroica kirtlandii) is one of the rarest of North American warblers. The nesting range is an area approximately 60x100 miles in the northern portion of the lower peninsula of Michigan. Within this very small range, nest habitat is confined to areas of sandy soils where groves of young jack-pine 5 to 18 feet in height occur. Habitat management seems simple: maintain open groves of jack-pine with proper ground cover. Wildfires formerly kept the pine canopy open and provided young trees. Special Kirtland warbler management units have been established within the limited breeding range. The Michigan Department of Natural Resources and the Forest Service have

reserved over 11,000 acres to be managed for this species. Tree removal and planting and controlled burning are being used to create the very specific environmental conditions needed for survival of the Kirtland warbler (Radtke 1963).

On the Los Padres National Forest in California considerable attention is being given to the California condor (Gymnogyps californianus). It is estimated that only 50 birds remain. The Forest Service has established two sanctuaries; in 1937, the 1200-acre Sisquoc Falls area protecting important bathing pools and several nesting sites and in 1947, the 53,000-acre Sespe Condor Sanctuary containing 90 percent of the nesting sites, bathing pools, roosting areas, and winter concentration areas. These areas are closed to all uses and public entry. A Condor Advisory Committee officially formed by the Chief in 1965 meets twice annually to advise on policy matters, discuss problems, and make recommendations to the Regional Forester.

The condor program is a cooperative effort between the Fish and Wildlife Service, California Department of Fish and Game, National Audubon Society, and the Forest Service. In 1974, a Condor Recovery Plan was completed and is awaiting approval by the Office of Endangered Species of the Fish and Wildlife Service.

The sole surviving population of Puerto Rican parrots (Amazona vittata) consisting of about 14 wild birds occurs on the Luquillo Experimental Forest in Eastern Puerto Rico. The Forest Service is cooperating with the Fish and Wildlife Service in research programs to determine habitat limiting factors. Improvement of nesting habitat by installing nest boxes is being investigated. Quality natural nest cavities appear to be a major problem. It is hoped that new populations can be established in other areas having suitable habitat.

The spotted owl (Strix occidentalis), listed as threatened, has received considerable attention on National Forest lands in California and Oregon. Old-growth timber logging and increased recreational use have been thought to be reducing the number of owls. Studies by State Fish and Game Departments, Universities, and the Forest Service were initiated in 1973 to determine status, distribution, specific habitat requirements, and concentration areas. In addition, agency personnel were trained to study spotted owls. Coordination guidelines were designed as follows:

1. Protect at least a 10-chain radius around each nest site.

2. Allow no clearcutting within 30 chains of a nest tree.

3. All cutting within 30 chains of a nest tree will be planned with a wildlife biologist.

The guidelines are minimal and serve as interim measures until the precise habitat use and relationships are better understood.

These examples illustrate the intensive kinds of management methods that must be developed if certain nongame species are to survive. Where the species territory is very small and habitat requirements very precise, identification of habitat and management will be a problem because of limited information.

NONGAME BIRD HABITAT PROGRAMS

The Forest Service has initiated both research and administrative studies to provide inventory, nesting habitat, and coordination technique information. Emphasis has been given to research and studies on the northern greater prairie chicken, bald and golden eagles, ferruginous and Swainson hawks, prairie falcon, mountain plovers, and osprey.

Osprey management areas have been created at Eagle Lake on the Lassen National Forest in California and at Crane Prairie Reservoir on the Deschutes National Forest in Oregon. Nesting poles and platforms have been installed to replace deteriorating snags. The response by the birds has been exceptional.

Annual surveys of northern bald eagle nesting success are being conducted for two purposes: to determine an index of annual production and locate active nesting eyries. Buffer zones of 10-chain radius are established around each known nest tree to prevent disturbance and protect the nest site. In Alaska the Forest Service has established the 10,000-acre Seymore Canal Eagle Management Area to protect this significant concentration of bald eagles.

In cooperation with the International Biological Program Study of the Shortgrass Ecosystem, a considerable number of studies are being conducted on the Pawnee National Grasslands. Studies on raptor populations include reproductive success of McCown's longspur, prairie falcon, golden eagles, Swainson and ferruginous hawks. This information is being utilized in the management of the National Grasslands.

The development of wetlands on National Forest lands for all inhabitants of this diminishing environment offer truly exciting opportunities. The Chippewa Wetlands Development

Program on the Chippewa National Forest in Minnesota, now in its seventh consecutive year, has improved the habitat and increased the numbers of nongame species as well as waterfowl. On the Modoc National Forest in northeastern California 1,500 acres of wetlands have been developed since 1966. Prior to these developments Forest Service biologists recorded 23 bird species while 2 years later, 160 species of birds were using the area. These two programs are only representative of what has been accomplished and what can be done to restore wetlands on National Forest lands.

Interest among the public and wildlife biologists in the general relationship between insectivorous hole-nesting birds and forest management has greatly increased. Insect damage in American forests is a significant cause of annual growth loss. As a component of natural biotic control, insectivorous hole-nesting birds can play a role in regulating forest insect populations. Without suitable snags, a large number of birds and mammals which depend upon snags may be lost. Coordination guidelines have been developed to leave enough older, mature, or overmature trees, often referred to as culls or defective trees, for the habitat requirements of these important birds. Several studies are underway to more precisely determine the number of snags required per acre and what type of snags are most beneficial.

Special areas have been established which comprise the most fundamental habitat requirements essential to a group of specific nongame bird species. Examples of some of these areas are:

1. Rock Creek Bird Nesting Site - 640 acres, Arapaho National Forest.
2. Sespe and Sisquoc Condor Sanctuaries - 38,000 acres, Los Padres National Forest.
3. Wetland Habitat Areas - 1,500 acres, Modoc National Forest.
4. Riparian Bird Habitat - 3,500 acres, Gila National Forest.
5. Kirtland's Warbler Management Area - 4,010 acres, Lower Michigan National Forest.
6. Strikine Waterfowl Management Area - 17,000 acres, Alaska.
7. Seymore Canal Eagle Management Area - 10,000 acres, Alaska.
8. Cooper Delta Dusty Canada Goose Area - 330,000 acres, Alaska.

Raptorial birds often use telephone poles, tree branches, and fence posts as perches in order to locate their prey. Research at Brigham Young University by Robert C. Christensen in 1972 indicated that it might be possible to control pocket gopher populations by installing pole perches and thus attracting birds to rodent concentration areas. The possibility of using biological control of rodents rather than toxic bait is a highly desirable approach. National Forests in California and Utah installed perches and are evaluating this technique.

Many of the National Forests have developed bird checklists. These lists are made available to Forest visitors and serve to point out the wide variety of species and habitat available on these public lands and to encourage visitors to become personally involved.

SUMMARY

Today, Forest Service wildlife programs emphasize nongame species more than ever before. The Endangered Species Act of 1973 has been one of the greatest influences on our wildlife efforts recently. However, we cannot forget the 800 or 900 other species which also depend on National Forest lands.

Nongame program development will be hampered by a lack of basic data for some years to come. However, we believe that we can significantly expand the Forest Service nongame program by in-Service training, cooperation with private and governmental agencies; conducting inventories, establishing priorities, literature reviews, and through the development of habitat simulation models.

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Management of Nongame Birds in Current Policies and Decision Making Within the National Park Service¹

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Abstract. Resources Management Plans determine project requirements and priorities. In 1974, sixty-six avian studies were undertaken within National Park Service areas. Project types include basic inventories, reintroduction of extirpated species, specific and general ecological studies, habitat analysis, and brush-fire studies.

There are few cases where the National Park Service directly manages its avifauna. There are numerous instances when a habitat management program is developed with birds in mind. The National Park Service administers to more than thirty million acres of land within the 50 states and the Virgin Islands. These lands contain not only some of the world's most spectacular scenery, but some of the most unique and wild environments known to man. The Service manages three basic types of areas--natural, cultural and recreational. It is charged to preserve its natural holdings in as near a pristine condition as possible. These areas may therefore serve as the last strongholds for many avian species, and act as ecological benchmarks for detection of environmental deterioration elsewhere.

National Park Service Policies

The policy of the Congress for the management and use of the national parks was clarified in the 1916 Establishment Act of the National Park Service, wherein it declared:

"The Service thus established shall promote and regulate the use of the Federal areas known as national parks, monuments, and reservations hereinafter specified by such means and measures as conform to the fundamental purpose of the said parks, monuments, and reservations, which purpose is to conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations."

^{1/} Paper presented at the Symposium on Management of Forest and Range Habitats for Nongame Birds, Tucson, Arizona, May 6-9, 1975.

It can be said that the National Park Service is not a conservation agency, but a preservation organization. Or its mission may be considered conservation in the sense of conserving resources that are not expressed in terms of money, but embrace the moral, spiritual, and educational welfare of the people and add to their joy of living.

The task of the Park Service is, in brief:

To manage the natural areas so as to perpetuate their character and composition.

To promote and regulate appropriate park use, and seek ever to improve the quality of that use; and

To provide the facilities required by the above in a manner complementing the character and special values of each area.

Administrative policies for natural areas of the National Park System (1970) have the following to say about plant and animal resources:

"Natural areas shall be managed so as to conserve, perpetuate, and portray as a composite whole the indigenous aquatic and terrestrial fauna and flora and the scenic landscape.

Management will minimize, give direction to, or control those changes in the native environment and scenic landscape resulting from human influences on natural processes of ecological succession. Missing native

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life forms may be reestablished, where practical. Native environmental complexes will be restored, protected, and maintained, where practicable, at levels determined through historical and ecological research of plant-animal relationships. Nonnative species may not be introduced into natural areas. Where they have become established or threaten invasion of a natural area, an appropriate management plan should be developed to control them, where feasible."

Resources Management Planning

The basic plan used by the National Park Service for documenting why and how its avian resources and habitats are managed, is the Resources Management Plan. A plan, prepared for every Park Service area, is initiated by the Park staff and coordinated by the Regional Scientist. It includes two major sections:

1. Project statements which identify the area's natural resource problems and management actions and area requirements to comply with Park Service natural science standards; and
2. Three-year programming sheets that include management costs, man-year needs, research priorities, and cost estimates.

Project types vary considerably. Those demanding resource studies include basic inventories; reintroduction of extirpated species; ecological analysis of unique species that may include those that are endangered, exotic, or of special scientific or visitor interest; ecological studies of a general nature; habitat identification and analysis; and brush-fire type studies of short-term nature.

Resources management projects are not so clear-cut because they usually are of habitat manipulation or of a nature that only indirectly effects the avifauna.

Management actions are almost always undertaken by the park staff. Research studies are most often conducted by University-based scientists, and only occasionally by National Park Service park area-based scientists.

Resource Studies

All of the park's research project priorities are combined into regional priority lists that serve as basis for funding requests. Approximately sixty-six avifaunal studies were conducted within National Park Service areas

during 1974. Ten of these were classified as basic inventories; two were studies to determine the feasibility of reintroduction of an extirpated species or monitoring of a reintroduction; twenty-two of the projects were ecological studies of endangered or unique birds; eighteen were studies of general ecological nature; twelve were habitat analysis directly relating to avifauna; and two were of brush-fire nature. Examples of each type of study follow:

An inventory of a park's resources should be completed at the earliest possible time. It is imperative for proper planning, management and interpretation. Some of the older parks, strangely enough, have never had a complete resources inventory. Some of these areas have been master-planned time and time again without a clear understanding by the planners of the resources that area is charged to preserve.

One of the newest of our national parks is Big Thicket National Preserve in east Texas. Preliminary surveys of the resources have already been completed and more intensive studies of the area's water resources, plant communities, herpetofauna and avifauna are now underway. In the case of Big Thicket National Preserve, planners and managers will have good resources data available to them prior to the time major decisions must be made.

Faunal inventories often document the need of reintroduction of extirpated species. Additional studies are then necessary to determine if environmental conditions are right for a reintroduction. Reestablishment studies usually command high priority in a park's list of natural resources projects.

The reintroduction of Montezuma Quail at Big Bend National Park will serve as a good example. Considerable study of the park's plant communities (Warnock, 1967 and 1969) showed that a great deal of natural rejuvenation of the grasslands occurred since the establishment of that park in 1936. The last park record of Montezuma Quail was in the early 1940s (Wauer, 1973a). Twenty-six birds were obtained from near Nogales, Arizona, in January 1973 and released in Pine Canyon of the Chisos Mountains the following day (Wauer, 1973b). Sightings of singing birds in Pine and Boot Canyons in May 1974 indicate that the restoration attempt was successful. Monitoring of this reintroduction will continue for at least two years.

Ecological studies of endangered or unique species comprised the most numerous avifaunal studies conducted within Park Service areas

in 1974. Among these projects were a Brown Pelican study at Channel Islands; Peregrine Falcon studies at Big Bend, Black Canyon, and Padre Island; Bald Eagle studies at Everglades, Yellowstone, Glacier, and Katmai; Spotted Owl studies at Sequoia and Yosemite; a White-tailed Ptarmigan study at Rocky Mountain; and a Cape Sable Sparrow study at Everglades.

Recent surveys by Wauer (1973) and Hunt (In Press) indicated that the greatest known concentration of nesting peregrines within the continental United States occur within the Big Bend country of west Texas. It is suggested that the resident populations of White-winged Doves may provide an adequate, relatively unpolluted food source within the isolated canyons and mountains to support as many as fifteen nesting pairs of this endangered species.

General ecological studies varied considerable. They included projects such as the energy balance of Common Ravens in dry heat at Death Valley, insect foods of Hawaiian birds, bird ectoparasites at the Virgin Islands, and Clark's Nutcracker behavior at Yosemite. At Padre Island National Seashore, Texas Tech researchers are studying the levels of chlorinated hydrocarbons in falcons.

Habitat analysis is underway at several parks. Scientists are studying niche requirements of juncos at Grand Canyon, nesting success on spoil banks at Padre Island, abundance and distribution of bird habitats at Cape Hatteras, avian habitat requirements at Guadalupe Mountains, and vegetation succession influences on nesting birds at Big Bend National Park.

The best example of a brush-fire type study was at Carlsbad Caverns National Park. Cave Swallows have nested at the caverns for several years, but the population was minimal and their presence at the cave entrance was hardly noticeable. However, when the Park Service changed the system of visitor access to the caverns from one of scheduled tours to that of allowing visitors to walk through the caverns at their leisure, this called for the continuous illumination of the caverns. Cave Swallows took advantage of the lighted passageways and their population multiplied from a few dozen to several hundred from 1970 to 1974. The swarming birds created a potential health hazard to the thousands of human visitors to the caverns, and maintenance of the walkways became a major concern. Quick recommendations to management were required. Scientists from New Mexico State University analyzed the situation (O'Brien, Robert T., and Ralph J. Raitt, 1974). Determinations to eliminate watering of the nearby plant life

and developing a microorganism monitoring program within the caverns resulted. The elimination of nest-building material was the logical solution to the problem.

National Park Service Management

Planning, management, and interpretation are all guided by a set of Park Service standards. The determination to manipulate the natural and cultural environments must be planned. When the suggested actions are controversial or significantly effect the environment, the public must be made aware of those considerations. Manipulations of natural systems must be precluded by scientific studies and analysis prior to the development of action alternatives. The Park Service natural science budget in 1974 amounted to about one and one-half million dollars. Although this amount is not sufficient to catch up with the multitude of backlog natural resource studies to do the job right, it is beginning.

Scientific studies conducted throughout the National Park System have considerably influenced management of the various ecosystems. Determinations of whether or not to develop or utilize particular locations is based upon potential environmental impacts of the proposed actions. The presence of a Peregrine aerie would preclude development nearby. The presence of a breeding population of Brown Pelicans on a small coastal island would preclude extensive visitation during the nesting season. The presence of resident Red-cockaded Woodpeckers within a particularly choice pine forest would preclude the use of that area for a campground or visitor center.

National Park Service policy toward the scientific collection of birds is addressed in the draft of the 1974 Administrative Policy in the following manner:

"At the discretion of the Superintendent, bona fide scientist and institutions may collect plants, animals, rocks, and other natural resource specimens when such specimens are not readily available outside of the area. Collecting (including the capture and release of marking of individual animals) may be an essential part of an approved scientific study. However, the collector must comply with all applicable State and Federal laws regulating collecting and associated activities. Casual and opportunistic collecting will be prohibited, and under no circumstances will collecting for personal use or profit be permitted.

Collecting by Service employees in the performance of their authorized duties shall conform to all applicable rules governing collection of specimens."

Each park has developed or is developing a park specific list of "restricted animals and plants." These lists include species for which parks will not issue collecting permits. The lists are based upon the following criteria:

- a. All wildlife and other biological resources which have been formally so recognized as "endangered" by the U.S. Fish and Wildlife Service and published in the Federal Register.
- b. All natural objects which are rare or endangered in a specific park regardless of their status in other areas administered by the National Park Service of their relative abundance in other sections of the United States.
- c. All natural objects or features which are rare or endangered in the park due to one or more type of ecological events or temporary phenomena. An example may be an extremely low population of a threatened peripheral bird species.

Specimens collected within parks must be deposited in a permanent public museum; or in the exhibit, study or type collections of scientific or educational institutions, unless the specimens are used up in the research. Specimens must be suitably recorded in a permanent file and must be available to the public. The park also has the right to designate where the specimen is to be deposited. In most cases the collector's affiliated institution will suffice, but the U.S. National Museum will serve as the depository for special specimens. It is especially important that all type specimens and those representing range extension and/or new state records be deposited in a large nationally recognized museum.

Conclusions

It has come through loud and clear at this symposium that the National Park Service represents a unique "breed of cats." Although preservation vs. use continues to be the Service's umbrella objective, additional management objectives for natural areas are usually distinct. Those basic objectives, that usually included in an area's enabling legislation, include language that the park's basic objectives include reestablishment of the area's natural ecosystems to the conditions that existed in 1790 or 1880 or whenever the first European arrived on the scene. Those basic directives preclude the necessity for an organizational raptor law, or channeling directive, or, in some cases, a forest insect or disease control program. Timber production,

game management and species diversity usually are unused terms to Park Service scientists and managers.

Our energy usually is directed toward other management objectives. We are more concerned with developing Resources Basic Inventories, visitor use analysis, backcountry management, natural systems preservation, and species reestablishment.

Climbing a little higher on the idealist's soapbox, I want to address an attitude with which most of you already agree. Natural parks are unique. This handful of vignettes of early America are worth preserving. There would be something terribly amiss with our political system if we could not choose 20 or 30 places that the American public could demand to be preserved in its entirety, and that management of those systems would be required only when negative human influences demand.

Those natural parks will serve not only as stabilizing influences for both scientists and laymen, but as ecological reference points to natural systems of the nation.

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Nongame Birds in Current Policies and Decision Making of the U.S. Fish and Wildlife Service¹

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Abstract.--The increasing involvement of the U. S. Fish and Wildlife Service with nongame species is discussed. Examples are provided of Service activities with nongame birds under the headings of endangered species, protection of wildlife environment, managing resources, research, law enforcement, federal aid, and cooperating with others. The Endangered Species Act of 1973 has greatly increased the Service's responsibility for nongame wildlife.

A Symposium on the management of habitat for nongame birds is timely, and of interest to the Fish and Wildlife Service. When we consider birds, the Fish and Wildlife Service carries a reputation for emphasis on the migratory waterfowl resource--occasioned, in large part, by the treaty acts and authorizing legislation. Because of Federal responsibility for migratory birds conferred by the treaties, and the fact that loss of wetland habitat created a crisis for waterfowl earlier than habitat loss affected most other groups of birds, it is natural that our management and research was initially directed to the waterfowl group. The Service has been giving increasing attention to nongame birds, as I shall indicate while discussing the role of this agency in serving wildlife and people.

The role of the Fish and Wildlife Service can be discussed under the headings of endangered species, protection of wildlife environment, managing resources, research, law enforcement, federal aid administration and

cooperating with others. I appreciate that time will not permit my covering each of these areas completely. I do want to highlight certain of these areas insofar as they relate to our activity and concern with nongame birds and particularly the topic of this panel.

Endangered Species

The Endangered Species Acts of recent years, culminating with the Endangered Species Act of 1973, has placed the preservation of endangered species and their habitats, including some of the nongame birds under discussion here today, as a number one priority of the Service. Through the identification of species that are either threatened or endangered, and placing them on the Secretary of the Interior's official lists, these species are provided with additional protection under the law.

Actions taken by this Service to insure the survival of species threatened with extinction include preservation and management of critical habitat, securing national and international cooperation, conducting research, initiating captive propagation programs where necessary, and enforcement of the Endangered Species Act. As examples of the Service's efforts toward preserving endangered or threatened nongame birds, we have in this Southwest Region a National Wildlife Refuge established

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to protect the Attwater's Prairie Chicken at Eagle Lake, Texas. Several of our refuges in the Southeast are managing woodlands for the red-cockaded woodpecker by utilizing longer rotations in the cutting of southern pine, or by preserving stands of the older, over-mature southern pine. This species has not fared well under current shorter cutting rotations, although industry is cooperating by identifying and preserving trees utilized by the red-cockaded woodpecker. Currently, thirty-nine endangered species are accommodated on the National Wildlife Refuges involving 136 individual refuges. The present refuge involvement in endangered species preservation is quite minimal in comparison to what the future may hold. If the current emphasis continues, "endangered species" may well become a dominant directive force in refuge management - thereby changing many of the current objectives relating to other species such as ducks, and to other activities such as recreation.

Attempts are also being made to restore the masked bobwhite quail through propagation and release into its original range on leased lands here in Arizona. This past summer the Service cooperated in an apparently successful attempt to condition and release propagated prairie falcons into the wild. This release was part of a national cooperative program designed to re-establish raptors in favorable habitat. We hope that this work with the prairie falcon will be a forerunner to a similar program with the peregrine.

Another interesting Endangered Species project is our work in cooperation with the Forest Service, the State of Michigan and the Audubon Society, toward preservation of the Kirtland's warbler. This warbler of the jack pine barrens of North Central Michigan reached an estimated all-time low of 400 individuals in 1971. The precipitous decline in the Kirtland warbler population occurred despite efforts to increase or, at least, stabilize the population by manipulating jack pine habitat in which the warbler nests almost exclusively through controlled burning and selective cutting. Through the efforts of the Kirtland's warbler Advisory Committee, it was discovered that another major factor in the warbler's struggle for survival was parasitism by cowbirds. The trapping and removal of 2,200 cowbirds in 1972 and 3,300 cowbirds in 1973 by personnel of the Fish and Wildlife Service and Forest Service on major

warbler nesting areas has resulted in an increase from .81 young fledged per nest to 2.84 young per nest. The 1973 spring census revealed that the Kirtland's warbler population had, in fact, "turned the corner" and estimates revealed an 8% increase over the 1972 population. Another problem with the Kirtland's warbler, disturbance by well-meaning bird watchers, is being handled by posting of the nesting areas and the supervision of warbler observation by Fish and Wildlife Service employees.

Protection of Wildlife Environments

Our Division of River Basin Studies reviews projects and environmental impact statements prepared by other agencies and is responsible for recommending against projects, or recommending redesign of projects where unacceptable impacts would result to wildlife.

The Division of Wildlife Services works with other landowners and managers, including Indian Reservations, military lands, and private lands toward the enhancement of wildlife habitat. Since most of the natural habitat in this country is controlled and managed by other agencies and by private individuals, these efforts have a considerable impact on the habitat of nongame birds.

Our Service monitors wildlife populations to evaluate the effects of pesticides, heavy metals, and other pollutants. All of you are familiar with the problem of thin egg shells due to DDT in the food chain, and the buildup of mercury through the food chain. Monitoring last year of the Tussock Moth Spraying area in Idaho, Oregon and Washington by our Denver Research Center Biologists indicated that DDT residue was more than doubled in kestrels within a mile of the spray area and increases were detectable in kestrels up to six miles from the spray area. The uptake of DDT and its metabolites is being determined from blood serum rather than fat or other tissue. This provides a considerable advantage in that the birds do not have to be killed and a series of samples from the same bird may be possible over a period of years.

Managing Resources

Our Service is the caretaker of over 360 National Wildlife Refuges, totaling 34 million

acres of habitat. Historically, refuges have been established for special kinds of wildlife, such as waterfowl, big game species of national significance, and endangered species. Thus, while habitat management and enhancement activities were directed toward benefiting such forms of wildlife, a land base and habitat has been preserved that benefits a broad range of other bird and animal life. Incidentally, the very first refuges were established for nongame species. Several of the refuges feature nongame birds—best illustrated by the Santa Ana Refuge in Texas. Public interest in many other refuges stems primarily from the nongame bird populations—including Great Swamp in N. J., Cape Romain in South Carolina, and Laguna Atascosa in south Texas.

A policy change in the late 60's initiated a program of setting individual refuge objectives which places a higher emphasis on managing for a maximum variety of species. Refuge Managers work toward the production of approved output levels and are discouraged from exceeding them to the detriment of any individual species. Since each different species accommodated under the item of wildlife diversity carries a very high rating, Refuge Managers are required to give consideration toward preserving or managing as great a diversity of habitat types as possible. While forest and rangeland birds have always been welcome on the refuges, they are thus being given a greater consideration in today's management of the National Wildlife Refuge System.

Under this same heading of Managing Resources, you may find the work of our Wildlife Services' field people of interest. Field personnel have been conducting daily eagle counts in our Region for four and a half years. This does not provide concise population estimates but does provide trend and concentration data, as well as indicate major population concentrations and time shifts which do occur. This may be a result of available food supply, but we don't yet know. We have seen golden eagle numbers build up in a particular area and then suddenly drop dramatically. However, another area will begin building in numbers as the previous one decreases. Naturally, this information provides insight into major wintering area and associated habitat.

For three years we have been making special efforts in conjunction with other agencies to locate, monitor and protect southern bald eagle nesting territories in our Region. From this work we now believe at least 95% of the active nests have been located. Although we have found no active nests in Oklahoma or New Mexico, there is a chance there may be one or two nesting pairs left in New Mexico. This nest location and production monitoring work is most often done cooperatively with other Federal and State agencies.

In the summer of 1973, habitat evaluation and avifauna investigations were carried out along sections of the Gila River in New Mexico and Arizona. One of the primary objectives of this work was to ascertain raptor habitat availability, raptor occurrence, and species composition in the more inaccessible canyon areas of the Gila River. This initial evaluation may be used as a guide for future attempts to reestablish certain raptor species in suitable habitat.

Our Division of Wildlife Services is often requested to provide help to commercial and military airports in relation to bird problems. This, again, is directly related to habitat and involves human safety. Most often the species dealt with are gulls, blackbirds, starlings and cowbirds. Occasionally, waterfowl, raptors, and other groups are the problem. Except for problems associated with low-level military flights and the conflict of migrating waterfowl, cranes and raptors with aircraft flight routes; most problems are directly associated with habitat, either feeding, roosting, or loafing. We generally work with the agency concerned, evaluate the particular situation, and then recommend habitat modifications to overcome the problem. This could involve closing or relocation of a garbage dump or planting and mowing practices associated with the airport.

Heron and egret roosting habits have also caused man-wildlife conflicts which we attempt to solve. Problems occur in urban or suburban environments where rookeries interfere with human activities. These problems must generally be solved by making the rookery move and, as a last resort, the roost site may have to be destroyed. Our input is in the form of evaluation and subsequent recommendations to the controlling agency or individual.

We also work with electric utility companies to solve raptor electrocution problems associated with power line poles. Power poles create a favorable hunting and loafing perch for raptors, especially eagles. This situation is favorable so long as the birds are not inadvertently electrocuted. Our work consists of identifying problem lines and then working with the company involved to modify the offending lines and poles to make them safe. Modifications may consist of changes in line spacing, insulation, addition of perches, changes in ground wires, or in one case, elimination of power in one of three lines of a three-phase line.

Conducting Research

Twenty years ago, much of the Service's research effort was expended on the behalf of waterfowl and in seeking solutions to economic losses caused by predators and rodents. With the increasing interest in endangered species and the loss of habitat through environmental degradation and pollutants, we have an increasing number of studies being made on the habitat needs of some nongame species.

These studies may be carried out by our Division of Research, or through grants to universities and other investigative agencies. National Wildlife Refuges frequently offer study sites for universities such as a study being carried out on the Attwater Prairie Chicken National Wildlife Refuge by Texas A&M University.

The Service also contributes to the considerable wildlife research being handled through our Cooperative Wildlife Research Units located at 45 universities throughout the country. An example is a study of the "Status and Ecology of Bald Eagles in Oklahoma" being carried out by the Oklahoma Cooperative Wildlife Research Unit. Habitat studies at the Oregon State Cooperative Unit revealed that the northern spotted owl was threatened with extinction because over-mature stands of Douglas fir--the only tree in which it nests--were slated for priority cutting at most timber operations. Forest managers are now aware of homesite preferences of the northern spotted owl and make allowances for its needs.

In 1973, we initiated investigations into the ecology of the golden cheeked warbler under contract with Texas A&M and, in 1974, with Stephen F. Austin University, Texas. The latter contract study is to determine the impacts of various forms of habitat manipulation on the bird and to determine more precisely the relationship of the warbler to ashe juniper. Prior to this study, it was believed the warbler required mature juniper trees (over 50 years old) to supply nest material. Although investigative results are preliminary, it appears that a much younger age class of tree (plus or minus 15 years) will satisfy the bird's needs. It also appears that solid blocks of trees are less acceptable and less used for actual nesting sites than those along the edge of natural or man-made openings. Earlier thinking indicated that large blocks of mature (75-100 year old) juniper were necessary for this bird.

Law Enforcement

The Service's force of agents works to prevent the exploitation of both game and nongame species. The importance of law enforcement and protection cannot be overemphasized. Even today the largest loss of eagles is due to indiscriminate shooting, despite the fact that the Bald Eagle Act of 1940 made the taking of eagles illegal.

Tremendous new responsibilities in law enforcement have been created by the Endangered Species Act.

Administering Federal Aid Programs

The Pittman-Robertson and Dingell-Johnson Federal Aid programs administered by our Service are primarily aimed at the benefit of game and fish and their habitat. Again, I would like to point out that the more than 4,000,000 acres of habitat procured by the States under these programs provides a considerable land base of preserved habitat that benefits our nongame species as well. Likewise, some of the research financed by the States through these Federal Aid programs is being directed to nongame species such as the studies being carried out by Texas on the Attwater's prairie chicken. Some states are financing the efforts of nongame biologists with these programs--such as is the case here in Arizona.

Cooperating with Others

Protection of the environment and the conservation of wildlife resources have become areas of concern worldwide. The tasks that remain to be done can be accomplished only through cooperative efforts involving all levels of responsibility: state, national, and international. I have frequently utilized the word "cooperation" today in discussing the Fish and Wildlife Service's role. One aspect I haven't touched upon are our responsibilities under the Sikes Act. Under the scope of our Sikes Act Cooperative Agreement with the military, we concluded a habitat management plan with the Army at Ft. Hood, Texas, which preserves key nesting habitat for the golden-cheeked warbler. This habitat contains stands of mature ashe juniper, the bark (strips) of which is required by this bird to construct its nests.

Prior to this action, the area was subjected to timber cutting, clearing, and miscellaneous military training exercises.

I believe the foregoing will indicate that the Fish and Wildlife Service has a deep concern for and is managing for nongame birds. I have with me some printed materials available from the Government Printing Office which also illustrate a trend in providing the public with information on nongame birds. Two of these, Attracting and Feeding Birds, and Homes for Birds, are revisions of pamphlets that were first published 25 years ago. A recent production is this Fifty Birds of Town and City, available from the Superintendent of Documents for \$1.20. Wildlife Portrait Series No. 3 has just been released and is comprised of 8 color pictures of songbirds.

Information Needs to Manage Forest and Range Habitats for Nongame Birds¹

Michael R. Lennartz² and Ardell J. Bjugstad³

Abstract.--This paper highlights the management information and research needs for nongame bird habitat management as pointed out in previous papers of this Proceedings. It also highlights comments submitted through letters from land managers. A consensus is implied that the management of nongame birds and their habitats is a relatively new resource issue and there is a veritable dirth of information available but badly scattered. Management has had difficulties defining goals and objectives for management.

INTRODUCTION

For the past three days we've all been involved in a continuing discussion of birds, bird habitats, and land management and an interest and need to manage lands for nongame birds. If there has been a consensus of fact and opinion, it is, perhaps, that management of nongame birds and their habitats is a relatively new resource issue and there is a veritable dirth of information for formulating and assessing management programs.

To start at the point of the information void would be a relatively easy, though time-consuming, task to list page after page of problem areas or questions in need of accelerated research to provide new knowledge and technology. But would research in all of the areas that could be identified be of equal interest and utility to the land manager, who is facing the challenge today of integrating nongame birds into his management planning? Obviously not, since with nongame birds, as

with all other natural resources, problems and opportunities must be met on a selective, priority basis.

Our attempt here is not to develop a comprehensive listing of all information needs that we could conceive, but rather to identify and discuss what we feel are high priority needs to facilitate management programs now and in the near future.

The ideas we express are not uniquely our own, although there is undoubtedly more subjectivity in our presentation than in most of the other papers presented during the symposium. We have relied heavily on the other symposium authors for suggestions and to identify significant gaps in the published literature. We sincerely appreciate the assistance we have received.

We also queried biologists with the Forest Service and the Bureau of Land Management regarding their program objectives for nongame birds and needs for new research and information. Their responses formed the focal points for our discussion. And we hope, that by the end of the day, another information source can be incorporated under this title--namely an open and vigorous discussion following this presentation.

MANAGEMENT OBJECTIVES

Any discussion of management information needs must necessarily follow some consensus or understanding of what management is or what management should strive to achieve. Does such a consensus exist for nongame birds? Shugart

¹Paper presented at the Symposium on Management of Forest and Range Habitats for Nongame Birds, Tucson, Arizona, May 6-9, 1975.

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et al. (1975) reminds us that wildlife research has traditionally emphasized game bird ecology and management, while generally ignoring the vast majority of other avian species. The reasons for this emphasis are indeed "pragmatic."

Game birds have tangible segment of organized public interest, i.e. hunters, hunter organizations, and sporting goods industries. This interest has been translated into political and financial support for game bird programs through legislation, taxes, and license fees. But the organized interest has aided the game manager in a manner other than support; it has provided relatively simple and clearcut program objectives. Regardless of the species in question, whether Ring-necked Pheasant in the Midwest, Ruffed-grouse in the Northeast, Bob White Quail in the South, or Chukars in the West, the challenge has been well defined: produce more birds, more hunter opportunity, and more hunter success. We do not mean to imply that meeting this challenge has been a simple task; indeed, some of the most sophisticated and noteworthy ecological research has been conducted on game species, and much remains to be done. Rather, we suggest that the rate of success we will have in managing nongame birds, will depend to a large extent (as it has in timber management, forage management, and game management) to the extent that related professions (ornithologists, wildlife scientists, foresters and range managers) agree, and work towards, common goals.

We suspect that while interest in nongame birds will continue to increase, such interest will be more diverse than traditional wildlife support, and it will behoove the professional, working in the public interest, to take the lead in establishing management and research direction. With few exceptions (e.g. endangered species) we can't expect a clear public mandate to establish this direction. Yet, without it we can't expect much public confidence or support.

Returning to a question we posed earlier: is there a consensus or general understanding of what nongame bird management is or should be? What value or product, in terms of nongame birds, should the land manager strive to protect or produce? Perhaps a consensus is too much to hope for, but from this symposium, and from our query to biologists and land managers, we feel two recurring and generally held philosophies have emerged for guiding forest and range management for nongame birds:

1. protect and enhance native vegetative communities or habitat types in order to protect and perpetuate all representative, native avian communities, and

2. protect and perpetuate endangered, and threatened species and their habitats.

If we accept these as broad management policies or objectives, what information do land managers need to meet them?

INFORMATION NEEDS

Native Habitat Types and Associated Avian Communities

A number of symposium authors have summarized and discussed the principles and patterns of avian diversity and the relationships between vegetative succession and diversity and avian succession and diversity (Thomas et al. 1975, Shugart et al. 1975 and Hamilton and Noble 1975). In a more general way, we have discussed the ways in which contemporary forest and range management systems affect vegetative communities and ultimately avian communities (Thomas et al. 1975, Hamilton and Noble 1975, Zeedyk and Evans 1975, Buttery and Shields 1975). Some of the salient points discussed in these presentations that are of particular importance in land management planning are:

1. bird species diversity changes in relation to plant succession (Hamilton and Noble 1975, Meslow and Wight 1975);

2. the pattern of avian succession is a manifestation of the habitat preferences and ecological requirements of the bird species (Shugart et al. 1975 and Balda 1975);

3. avian species diversity is often positively correlated with the diversity in form and density of vegetation layers (Hamilton and Noble 1975, Shugart et al. 1975, and Thomas et al. 1975, Meslow and Wight 1975 and Myers and Morris 1975);

4. foliage diversity and avian density and diversity tend to increase as succession proceeds (Hamilton and Noble 1975, Shugart et al. 1975, Meslow and Wight 1975);

5. in an individual forest stand maximum avian diversity and density is often found at or near climax or maturity, but for an entire forest the most diverse and dense bird populations are often found at an ecotone or edge of contrasting vegetative types (Hamilton and Noble 1975, Shugart et al. 1975);

6. forest and range management practices affect avian communities positively or negatively, primarily through alternations in form and density of the vegetative layers that comprise avian habitats (Thomas et al. 1975, Buttery and Shields 1975);

7. management practices that tend to simplify vegetative structure, vertically or horizontally, create less diverse habitats which in turn support less diverse avian communities (Hamilton and Noble 1975, and Thomas et al. 1975, Meslow and Wight 1975); and

8. few land management practices absolutely destroy avian habitats, most modify or alter the vegetation and associated avian community, and the change is only detrimental or advantageous relative to specified management objectives or some desired distribution of avian communities through time and space (Hamilton and Noble 1975, Zeedyk and Evans 1975, Thomas et al. 1975, Buttery and Shields 1975).

How do these general tenets help the manager meet his objective of protecting and perpetuating habitat heterogeneity and native avian communities and what more specific information is needed? We can approach this question from two angles--in a sense, one negative and one positive.

Taking the negative first, one of the most pressing needs expressed by managers is information and methodology which would allow them to assess, in quantitative terms, the impacts of management systems on nongame birds and their habitats. Several symposium papers have described the general patterns of impacts exerted on avian habitats and communities by intensified land management e.g. truncated succession, loss of old growth habitats, loss of snags and cavity trees (Thomas et al. 1975), and decreased vegetative diversity with monoculture systems in timber or range management (Hamilton and Noble 1975, Buttery and Shields 1975). These general patterns focus attention on major problem areas, but much finer focus is needed.

If forest and range management practices tend to upset natural succession and replace certain successional stages with others, then one of the first needs for assessing impacts is a knowledge of the avian species commonly associated with the major seral and climax stages of vegetation succession. Studies similar to those by Johnston and Odum (1956) in the Georgia Piedmont and Shugart and James (1973) in the Ozark Highlands provide managers the basic avian resource information with which to assess their own management efforts. Traditionally, such efforts have concentrated on breeding bird populations. But, as Wiens and Dyer (1975) have pointed out, habitat alternations in wintering areas may exert a considerable influence on a given breeding population. Thus, as habitat managers, our information will be incomplete and confounded unless research includes wintering and migrating as well as breeding populations (Sprunt 1975).

Early and late successional stages of vegetation require particular attention, since these are the communities intensive land management tends to segregate against--particularly the climax communities. Beyond these primarily descriptive efforts there is a need to accelerate research using multivariate analyses, as discussed by Shugart et al. (1975), to quantitatively explain the distribution and habitat selection of avian species and communities. We stress both species and communities, because as Balda (1975) has pointed out, neither autecological or synecological studies alone can adequately describe the patterns and processes of habitat selection and resource utilization. Both approaches are needed, and multivariate approaches provide the means to most efficiently assimilate and analyze the vast amount of information needed. As we gain knowledge, not only of what species we can expect to occur in a given habitat, but also of what factors in a particular habitat influence habitat suitability for the associated avian community, we gain the ability to purposefully manipulate forest and range vegetative communities to accommodate a particular bird species or community. Many managed forest and range vegetative communities alter, rather than replace, naturally occurring successional stages. If the land manager knows the proximate and ultimate factors in habitat selection, he can incorporate the structural elements of critical avian micro-habitats into landscapes managed primarily for other resource outputs e.g. lumber, fiber, cattle, forage, etc.

As we move from the need to assess impacts to information needs to facilitate active management of nongame birds, we move from the negative to the positive. We hasten to add, however, that impact assessment need not necessarily bear a negative connotation. Perhaps, with the knowledge to anticipate losses, we gain the ability to predict and manage to prevent them.

It is probably true, as Hamilton and Noble (1975) and Buttery and Shields (1975) have stated, that in most cases avian management on our forest and range lands will be in conjunction with other management objectives or other resource outputs e.g., timber and forage. We should not infer, however, that avian management planning can be more hazardous or less sophisticated than planning for the "primary" resource outputs. And with increased information on birds and their habitats, it need not be. The most basic, indeed the first, information required in land management planning is some characterization of the extent, distribution, and condition of the resource base. Foresters utilize various continuing forest inventory systems to periodically assess conditions and trends

of the timber crop. As we gain more knowledge of what bird species are associated with what forest types and successional stages, and of the factors that influence habitat suitability, it should be possible to incorporate avian habitat assessments into existing forest inventory systems.

Biologists on most National Forests along with state and institutional biologists are at work developing classification schemes for understory vegetative communities in an effort to expand the utility of inventories and surveys to assess wildlife opportunities as well as timber potential. The feasibility and utility of such habitat assessment systems will be in direct proportion to the amount of information available. Information will be needed on avian community/plant community associations and quantified parameters of habitat selection and suitability. Coupling such a habitat assessment system with the monitoring of selected indicator species as suggested by Verner (1975) and the National Breeding Bird Surveys as outlined by Peterson (1975) offers a comprehensive and practical solution to the problem.

We recognize the need for the sort of information we have outlined for all major habitat types, whether natural or culturally altered. Realistically, however, we suggest the initial or accelerated emphasis be placed on the communities where the greatest management problems exist. As noted earlier, considerable concern already exists for climax or mature vegetative communities and their associated avian communities. There appears to be general agreement that the mature systems are being lost at an increasing rate and will probably not be replaced during successive managed rotations or cycles. At the same time, we have very little information on specifically what is being lost, in terms of habitat birds and other environmental values, or whether or not management could ameliorate or compensate the losses. We know that snags and cavity trees are eliminated as forest management intensifies with shorter rotations, thinnings, and sanitation cuttings. But what do we lose in terms of avian habitat when we lose snags (or other micro-habitat elements, for that matter) and how can the loss be minimized or avoided? How many snags per unit area of land are desirable and in what juxtaposition with other vegetative elements.

There may come the day, when demands for economic resource outputs from forest and range lands force such intensive management practices that maintaining large, extensive

acres of mature or climax vegetation will be precluded. Yet, we hope that managers, at least on our public lands, will always strive to provide for some significant acreage in these habitats to protect avian, wildlife, and other wildland values. Before then, we will need information regarding the minimum acreage required to sustain representative avian communities, the minimum number of breeding pairs needed to perpetuate a population, and the optimum pattern of dispersion for these habitat islands and perhaps for some species interconnecting corridors to protect against extinctions. Which brings us to endangered species.

Endangered and Threatened Species

Conceptually, the information and research needs for endangered species are no different than those for other avian species or communities. We need the same information on habitat association, habitat selection, resource utilization, habitat population distribution and trends, limiting factors, and management guides. But the needs are more urgent.

Almost without exception, the managers and biologists we queried responded that information on habitat requirements and management for endangered and threatened species was their highest priority. Some would argue that endangered species are demanding too much attention, sapping resources from other wildlife problems badly in need of new research and management efforts.

Without caring to enter the debate, we will only add that there are a number of very pragmatic reasons for emphasizing and giving priority to endangered species. First, the plight of species headed for or faced with extinction has received a great deal of public attention, and has become one of the most publicized contemporary wildlife management issues. Second, this interest, whether objective or subjective, intellectual or emotional, has been translated into public program support through legislation (Endangered Species Act of 1973). Admittedly, as Grieb and Graul (1975) have pointed out, not all the support planned has yet materialized, but the foundation has been laid. And finally, the Endangered Species Act requires that all federal, or federally funded, land management programs protect endangered species and their habitat (Endangered Species Act of 1973). To do so requires much additional information on habitat requirements, critical habitat parameters, and species and habitat response to vegetative manipulation.

The endangered species experience holds a lesson for other nongame bird programs as

well. Although wildlife programs have traditionally emphasized game species, most wildlife management agencies recognize the need, and are committed to developing, programs for nongame species as well. But expanding a wildlife program and moving off into new areas of endeavor require new sources of support, new funding, and often new legislation.

The impetus behind endangered species programs has come from enlightened concern regarding man's role in species extinction, the accumulation of knowledge and information to assess the problem and awaken public interest and concern, and finally public response and support in the form of legislation. We should recognize, then, that the degree of support and funding for other nongame programs will depend upon the degree to which the programs satisfy some human need. But before we can attempt to satisfy needs we must be able to identify them.

Essentially, the question we need to answer is how do we justify programs of research and management for nongame birds? If we are acting in the public interest, who is our public and what are we striving to provide? The committee on North American Wildlife Policy summed up the research challenge when they stated: "Our most neglected and crucial research needs are those concerning human social behavior.... We have long bewailed our inability to "reach" the general public with facts and create a better understanding of sensitive management issues.... Or how to serve best the long-term interest of the people.... The biologist alone, the social scientist alone, the economist alone cannot deal with these questions. Their combined effort is required, and it must do great things (Allen 1973)."

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Discussion

MS. DANFORTH: Where do we go from here? Is there going to be a coordinating body for non-game bird species, coupled with an information system?

MR. SCHNEEGAS: I believe there are some efforts underway with the research people in the Forest Service to pull some data together.

DR. SMITH: The Forest Service is working with other Federal agencies and with the States to develop some type of information system for all

wildlife. You've heard many references to the fact that the literature is badly scattered. This symposium is one step towards synthesizing that vast body of information. The automated information system may be some distance into the future, but I am quite confident that one will be forthcoming. Another step from here is the possibility of taking the results of this symposium and organizing a series of regional seminars for States and land management agencies.

Concluding Address:

The Challenges of Management of Nongame Birds¹

Lee M. Talbot^{2/}

The concluding speaker always operates under a set of extremely adverse environmental impacts. It is always the end of a long meeting. Everyone is tired; some of the audience have gone home. Those who are left -- and who are still awake -- are impatiently contemplating the flight home or the evening drink. They are all listened out. What they don't need is more platitudes -- but that is what they expect.

Most concluding speakers are subject to the same set of influences -- the difference being that they are expected to speak. Normally, they produce the expected platitudes:

The conference participants are distinguished.

The meeting a milestone; the results significant.

The sponsors deserving of great credit for assembling such a distinguished group to deal so well with such a significant subject.

All right, consider it said, and I have done my expected duty.

However: As this symposium comes to a close, there are several major points which deserve emphasis. The first of these is that this meeting has been an extraordinarily long time in coming. Aldo Leopold and other pioneers in wildlife management spoke of wildlife as a whole, not of wildlife solely in terms of game. Even in the Preface to his classic "Game Management," Leopold said that his objective was "to portray the mechanism which produces all species on all lands."^{3/} However, in the development of the practice and profession of wildlife management, the broader foundations were forgotten and the focus has been ever more narrowly on game as

such, and the production of a shootable surplus.

This is understandable and, perhaps, inevitable. Until recently hunters have been the most effective national wildlife constituency. They still remain the major source of wildlife management funds. Like other resource management professions, wildlife management developed in response to the demands of the particular constituency which wanted that resource, i.e., the hunters. To a large degree, the principles and practice of management, the institutional and funding arrangements, and the teaching of practitioners, all developed in this mode.

However, the rapidly growing environmental awareness of the past decade has created a whole new wildlife constituency...new in terms of numbers and new in terms of demands. While hunters comprise 5 to 10 percent of the population, present estimates indicate the great majority of Americans have an active other interest in wildlife. The present demand is for a broad spectrum of values from wildlife other than the production of a shootable surplus. This new interest is often less focused and less well informed than the interests of hunters, but it extends far beyond the narrow spectrum of game species. Directly or indirectly, it extends to most of the nation's 400 forms of wild mammals and 800 species of birds.

This new demand and its implications have been discussed earlier in this symposium, and dramatic figures cited which indicate the economic magnitude of the nongame bird ball game. However, in spite of all this, the narrow focus on game of the wildlife professions remains remarkably persistent, and it is important that we not underestimate the challenges this fact poses to accomplishing the objectives of this symposium.

Institutions and professions change slowly. They are seen by the public to change more slowly, perhaps, than they actually do. However, the public's broadened interests and aspirations for wildlife have not yet been met by the broadening of the focus of wildlife management, and the public realizes this. Associated with this is an increasing polarization between hunters and nonhunters. Hopefully, this symposium can be a major

^{1/}Concluding Address at The Symposium on Management of Forest and Range Habitats for Nongame Birds, Tucson, Arizona, May 6-9, 1975.

^{2/}Assistant to the Chairman for International and Scientific Affairs, President's Council on Environmental Quality, Washington, D. C.

^{3/}Leopold, Aldo. 1933. Game Management. Charles Scribners Sons, New York. 481 pp.

contribution to broadening the profession as well as to broadening the perception of the profession by the public.

In my frequent travels around the country, I have occasion to meet with wildlife managers in the field and with wildlife students and those who teach them in the universities. I am increasingly concerned that far too many wildlifers still do not appreciate the magnitude of the shift in the orientation of their constituency and their responsibilities, from hunting to nonhunting. Their failure to recognize or respond to this situation constructively, and worse, the outspoken defensiveness of many wildlifers, has created a real credibility gap between them and the public. In 1972, Dan Poole spoke eloquently about the problem in his introduction to the North American Wildlife and Natural Resources Conference in Mexico City. It is still with us.

I said that the narrow focus on game was persistent. Let's examine that premise. In 1968, the Bureau of Sport Fisheries and Wildlife convened a Symposium on "Man and Nature in the City" with the aim of exploring the role of nature in the urban environment, and more particularly, exploring what the role of the wildlife manager should be relative to that nature. This was really a pioneering effort in the context of wildlife management at that time. Unfortunately, it was not followed by much action. In the following year, less than 4 percent of the total wildlife funding from all sources -- federal, state, and private -- went to clearly nongame purposes.

Since then, there have been nongame efforts by the wildlife profession and the government. I could cite the revised North American Wildlife Policy, the Model State Non-Game Legislation developed by the International Association of Game, Fish and Conservation Commissioners, and Wildlife Society, and the CEQ-Department of Interior studies to explore nongame funding and policy, changes in name and some changes in emphasis by federal and some state wildlife agencies, federal legislation such as the new Endangered Species Act and Marine Mammal Protection Act, as well as the increased consideration to nongame wildlife required by the National Environmental Policy Act. Yet in spite of all this, the actual situation has changed relatively little since 1969.

In the current fiscal year, 3.5 percent of total wildlife management funds of 13 Federal agencies is directed to nongame wildlife, as is roughly 1/4 of their research funds. The figure is even lower in the state

agencies. This fiscal year, in the states, nongame wildlife received 1.0 percent of management funding, 4 percent of research, and 2 percent of law enforcement.^{4/}

It is clear that we must develop the budgetary and legislative foundations for a nongame wildlife program which will be essentially parallel to and complementary with the present game-oriented wildlife programs. Yet it is equally clear that we cannot wait for all that to occur; there is still much that we can do within our present legislative and budgetary constraints and this symposium has provided important impetus and guidelines for this action.

A further significance of this symposium comes from its joint sponsorship with representatives of private organizations, federal and state agencies and universities. We are dealing with federal, state, and private lands, with a resource which does not recognize boundaries, and with a set of programs involving all of these sectors. There is no way that one single agency or institution can deal effectively with the problem. Yet, most attempts so far have not involved this spectrum of groups, and I find this symposium effort particularly hopeful because it does. It is hard to overemphasize the importance of continued Federal-State-private teamwork in nongame management. A related point is that, as far as I know, this is the first time that avian ecologists have really gotten together with the land managers who are responsible for their birds. It is hard to overestimate the significance of this development also.

The basic thrust and objective of this meeting is an additional point that deserves emphasis. Basically, this was intended to be a "state-of-the-art" exercise. Inevitably there is far more known about our subject than there is applied. Much of the research that has been done is not published or is scattered in a variety of journals. More important, much has been published in scientific form, not in an operational form which the managers can use. While it is true that more research is needed, new research undertaken without reference to the body of existing but unused data simply runs the risk of reinventing the wheel, and worse, of delaying the day when something effective will be done. Therefore, major need is to identify and bring together existing knowledge, synthesize it, and present it in the

^{4/}Wildlife Management Institute, 1975. Current investments, projected needs, and potential new sources of income for nongame fish and wildlife programs in the United States. 94 pp.

form that is useful to those who need it. From this perspective, the approach taken at this symposium has promise of a really solid contribution.

The major thrust of the technical discussions during the past three days has been on the habitat, or ecosystem approach. This approach has been a major contribution of the United States to wildlife management in general. I believe it is significant that in his "Game Management," Aldo Leopold emphasized this point specifically with reference to our subject saying, "this is the substance of game management, and can likewise become the means whereby each community creates its own dearth or abundance of nongame birds." (Leopold, 1933, p. 405)

Yet viewed in this perspective, it is ironic that the ecosystem approach has been so very little employed in management of the world's terrestrial and aquatic wildlife. This was a major conclusion of a program of meetings and workshops on management of the world's wild living resources which has just been completed in Washington. The major recommendation of that distinguished group was that wildlife management must focus on the ecosystem, not on a single species in isolation. The approach of this symposium indicates that for nongame birds, in terms of the conceptual basis for management,

at least, we are really ahead of the long established practitioners and practices of wildlife harvest. Our challenge, then, is to apply this conceptual framework effectively.

Clearly, we need much more information on the species and ecosystems involved, but I would reiterate that much is already known which can be applied. The challenge here, then, is two fold: For research -- since so relatively little really has been done on most of our nongame bird species -- and for application of what we do know.

I believe we are at a critical point in the history of wildlife management. Wildlife and wildlife habitat have never had such severe challenges as those which our increasing population and technology are now providing; there has never been such strong public and legislative support for wildlife; nor such strong skepticism about the ability of the wildlife profession to manage it. I believe, however, that the efforts of this symposium have made a significant contribution; if we can implement well what has been presented here, it will contribute significantly to an effective, balanced wildlife program. With this type of approach the wildlife profession itself can emerge greatly strengthened and ultimately the nongame resource can be well managed.

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Smith, Dixie R., Technical Coordinator

1975. Proceedings of the symposium on management of forest and range habitats for nongame birds. [May 6-9, 1975, Tucson, Ariz.] USDA For. Serv. Gen. Tech. Rep. W0-1, 343 p. Wash., D.C.

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